Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight

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Abstract

We compiled a global data set of copepod in situ weight-specific fecundity and growth rates, together with measurements of their body weights, and the chlorophyll *a* and temperature of the natural water in which these animals were growing. Juveniles can achieve half-saturation of their growth (K_m) at chlorophyll *a* concentrations almost an order of magnitude lower than adult females can their weight-specific fecundity. Adult weight-specific fecundity rates in situ are correlated with temperature, but the Q_{10}s of 1.59 and 1.43 in broadcast and sac spawners, respectively, are much lower than under food saturated laboratory conditions (Q_{10}s of 2.75 and 3.98). By comparing the in situ and laboratory food saturated results we are able to assess food limitation in the environment. The degree of food limitation increases with increasing temperature for adults; in situ rates approximate food saturated rates at low temperatures (0–10°C), at 25°C they are on average only about one-fifth of those at food saturation. By contrast, in situ juvenile rates are more strongly temperature-dependent than their adults and close to food saturation even at high temperatures. Juveniles grow much more rapidly and closer to food saturation than do adults of a similar size. There are several possible reasons for this. Compounds needed for egg production may simply be more dilute than those used in somatic growth. However, it is also possible that food limitation acts very differently in adults than juveniles. Molting rates in juveniles are strongly temperature dictated, and if sufficient weight is not added between molts, these slower growing juveniles do not survive. Adults, by contrast, can survive for long periods without having sufficient food to produce eggs.

Copepods are the dominant mesozooplankton in the marine environment, comprising as much as 80% of its total biomass (Kiørboe 1998). They are important grazers of phytoplankton and microzooplankton (Atkinson 1996) and form a major trophic link to many predatory invertebrates and fish. Copepods also play a fundamental role in the upper ocean—exporting, redistributing, and repackaging carbon and nutrients (Banse 1995).

Weight-specific fecundity and growth are key parameters—descriptors of the rates at which copepods process material, these terms also relate to their potential to supply energy and matter to higher tropic levels. Productivity has become a central and extensively studied aspect of marine plankton research over the last few decades (Runge and Roff 2000). Although egg hatch and postembryonic development times show strong temperature dependence in a wide range of animal groups, including zooplankton (Peterson 2001; Gillooly et al. 2002), these rate processes are largely free from food limitation. Postembryonic development times can be biased toward the fastest growing (least food limited) animals as a result of methodological bias (Carlotti and Nival 1991; Hirst and Sheader 1997). Additionally, slower growing more food-limited individuals may never make it to adulthood (Lopez 1991) and so are not included in a measurement reliant only upon those individuals that do. Development times have to some extent biased our appreciation of the role food control plays in the natural environment. Food-limitation in the natural environment may act to suppress growth, fecundity, and development rates in different ways and to varying extents.

Growth and fecundity measurements are time consuming and labor intensive, consequently only a small number of species have been studied in any detail. Even the most extensive investigations of growth and fecundity can measure rates in only a few species stages (e.g., Peterson et al. 1991; Hopcroft and Roff 1998*a*; Gómez-Gutiérrez and Peterson 1999), while the vast majority of investigations are on just one (e.g., Ambler 1986). Current approaches for measuring zooplankton growth and production make it impractical to make comprehensive measures (including most species and stages present) over large areas with high spatial and temporal resolution. If we are to map these processes, there is a need to be able to either measure or predict these rates more comprehensively and at higher resolution. Predictive models that allow derivation of growth from more easily measured parameters such as temperature (Huntley and Lopez 1992) or temperature and size distributed biomass (Ikeda and Motoda 1978; Hirst and Lampitt 1998) have been developed.

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Hirst and Lampitt (1998) used a large data set of in situ adult and juvenile growth measures to construct models based on temperature and body weight. Predictions from these empirical relationships give reasonable estimates (Roman et al. 2000, 2002; Richardson et al. 2001; Peterson et al. 2002). However, their model, as well as those of Huntley and Lopez (1992) and Ikeda and Motoda (1978), does not incorporate food resources. Quantity and quality of food clearly accounts for variability we observe in copepod growth and egg production rates in nature and may be expected to be a primary reason for some of the mismatch between predictions and field measurements (*see* Calbet et al. 2002; Peterson et al. 2002). Both the Hirst-Lampitt and the Huntley-Lopez models overestimate growth rates for oligotrophic areas (Calbet and Agustí 1999), and this is primarily the result of their bias toward data from food-rich areas and periods. A logical and necessary progression is the inclusion of a food descriptor. Although Huntley and Boyd (1984) included a food proxy (as total μg C L^{-1}) in their growth model, their predictive relationships are only applicable over a very restricted body weight range, i.e., 0.01–0.10 mg dry weight (DW) per individual (ind^{-1}), thus precluding their use for many animals in most environments. Although it has been applied outside this body weight range (e.g., Davis 1987), the relationships are generally counterintuitive beyond the limits, and conclusions drawn are likely to be in error.

Copepod diets can be selective and diverse, and they can vary spatiotemporally and ontogenetically. They often include not just phytoplankton but heterotrophic flagellates and ciliates, detritus, and other metazoans, and they can feed cannibalistically. Selectivity by copepods may relate to the size of the prey (Atkinson 1996), its toxicity (Huntley et al. 1986), and nutritional quality (Houde and Roman 1987). Motility, swimming, and escape behavior of the prey are also important (Atkinson 1995), as are the detection methods, feeding tactics, and abilities of the copepods (Paffenhöfer and Mazzocchi 2002). Measurements of food concentration in the water do not necessarily represent prey ingested, assimilated, and ultimately ability to sustain the growth and fecundity of copepods. Historically, many different terms related to copepod ingestion, growth, and physiology have been used in describing the food environment. These have included chlorophyll *a* (Chl *a*), particulate organic carbon and nitrogen concentrations (McKinnon 1996), microplankton counts (McKinnon and Ayukai 1996), and biochemical measures such as fatty acid composition (Pond et al. 1996). Total and size fractionated subsets of the total have been used; the latter in order to account for the fact that copepods are restricted in the size of prey they take. Hansen et al. (1994) found optimal clearance by copepods to be at a predator–prey equivalent spherical diameter ratio of ~18 : 1. Unsurprisingly, growth and fecundity are therefore often better correlated to size fractions of Chl *a* than its total concentration (e.g., Runge 1985; Ambler 1986; Peterson and Bellantoni 1987; Uye and Murase 1997), specifically subsets that exclude the smallest fractions (e.g., >5 μm, >10 μm, or >20 μm). Previous published relationships between weight-specific fecundity and growth and food proxies are presented in Table 1.

By far the most common (and almost universal) measure of the food environment of copepods continues to be Chl *a*. Although in some instances no correlations between growth/fecundity of copepods and Chl *a* concentration have been found, significant positive relationships have been reported in a diverse range of species and environments. These significant relationships include polar (Hirche and Bohrer 1987; Lopez et al. 1993; Shreeve et al. 2002), temperate (Durbin et al. 1983; Kiørboe and Nielsen 1994), and tropical waters (Hopcroft and Roff 1998*a;* Hopcroft et al. 1998), and from shallow estuaries/lagoons (Landry 1978; Ambler 1986; Beckman and Peterson 1986) to upwelling (Peterson and Bellantoni 1987; Hutchings et al. 1995; Richardson and Verheye 1998) and oligotrophic open ocean regions (Calbet and Agustí 1999). Chl *a* is a general indicator of the trophic condition of an ecosystem, albeit an imperfect index of the food used in growth and fecundity. On a global (Legendre and Michaud 1999) and a local scale (Durbin et al. 1983) total Chl *a* can relate strongly to particulate organic carbon (POC). Some ciliates also contain Chl *a* (e.g., *Mesodinium*, *Strombidium*, and *Tontonia*), while heterotrophic ciliate biomass positively correlates with phytoplankton (Nielsen and Kiørboe 1994). Total Chl *a* also has the advantage that it can be estimated rapidly using fluorometric instruments and remotely over large areas from satellites. However, as Table 1 demonstrates, there has been little standardization on the location at which food is measured in the water column or the equation forms chosen in expressing relationships between food proxies and weight-specific fecundity or growth. There were, therefore, a multitude of reasons why we chose to use a standardized Chl *a* term as the food-proxy descriptor here. We fully accepted that other food proxies may eventually prove to be far superior in relation to growth and fecundity, but at this stage we have little alternative in a global synthesis of this nature.

The principal aims of this study were as follows:

1. To examine how weight-specific fecundity of adult (copepodite-VI females) and weight-specific growth of juvenile (nauplii-I-CV) marine copepods in the field relate to Chl *a*, temperature, and body weight in broadcast and sac spawners.
2. To relate in situ weight-specific fecundity and growth to those measured under laboratory food saturation and thus explore the degree and pattern of food limitation in the different groups.
3. To increase our ability to predict copepod in situ weight-specific fecundity and growth rates using Chl *a* (where appropriate).

Methods

In situ weight-specific fecundity and growth—Data compilation: The published literature was searched for growth and egg production rates of marine planktonic copepods. Screening criteria were designed so as to select results where the rates were likely to reflect in situ conditions. We included only those studies where recently caught individuals were incubated for ~24 h. Data were included if the temperature of incubation was close to that found in situ (i.e., within 5°C

Table 1. Published relationships describing weight-specific fecundity of adult females and weight-specific growth of juveniles (g, d^{-1}) as a function of the concentration of food proxies for marine planktonic copepods. In some instances temperature (T, °C) and body weight (μg ind^{-1}) (DW = dry weight, CW = carbon weight, and AFDW = ash free dry weight) have also been included. Animals were collected from the environment and immediately incubated in natural seawater, except those in bold, which were fed natural seawater but prey were stored or their concentration altered by dilution. Those in italic are studies under artificial laboratory conditions. Letters in equations refer to resource descriptors—*see resource descriptor annotations below.** ln signifies $\log_e$, log signifies $\log_{10}$, In many cases authors have not given equations when relationships are not significant, and hence these cannot be included here.

Species (stage)	Relationship: weight-specific fecundity/ growth (d^{-1})	Temperature (T, °C)	r^2
***Acartia omori* (C6♀)**	**(66.2A)/(0.470 + A)/100**	**15**	**—**
***Acartia steueri* (C6♀)**	**(80.0A)/(0.912 + A)/100**	**20**	**—**
***Acartia tonsa* (C6♀)**	**0.41M + 0.04**	**23**	**0.81**
***Acartia tonsa* (C6♀)**	**0.50M + 0.05**	**24**	**0.77**
***Acartia tonsa* (C6♀)**	**0.09M + 0.17**	**27**	**0.77**
***Acartia tonsa* (C6♀)**	**0.04M + 0.28**	**14–19**	**0.52**
***Acartia tonsa* (C6♀)**	$\mathbf{(0.058}T\mathbf{ - 0.015}S_a\mathbf{ - 0.037}U_a\mathbf{)\ (1 - }e^{-1.13M}\mathbf{)}$	**14–28**	**—**
Calanoides carinatus (C6♀)	$0.194\ (1 - e^{-0.160P})$	?	0.24
Calanus agulhensis (N6)	$0.593\ (1 - e^{-4.614P})$	14.8-20.5	0.27
Calanus agulhensis (C1)	$0.635\ (1 - e^{-2.580P})$	11.5–20.4	0.13
Calanus agulhensis (C2)	$0.552\ (1 - e^{-2.010F})$	11.5–21.4	0.19
Calanus agulhensis (C3)	$0.373\ (1 - e^{-1.222P})$	13.2–21.5	0.15
Calanus agulhensis (C4)	$0.399\ (1 - e^{-0.648P})$	9.5–22.8	0.24
Calanus agulhensis (C5)	$0.124\ (1 - e^{-0.998P})$	9.5–22.8	0.04
Calanus agulhensis (N6)	$0.550\ (1 - e^{-4.827P})$	?	0.05
Calanus agulhensis (C1)	$0.612\ (1 - e^{-1.970P})$	?	0.11
Calanus agulhensis (C2)	$0.551\ (1 - e^{-1.435P})$	?	0.17
Calanus agulhensis (C3)	$0.400\ (1 - e^{-1.035P})$	?	0.22
Calanus agulhensis (C4)	$0.396\ (1 - e^{-0.501P})$	?	0.26
Calanus agulhensis (C5)	$0.144\ (1 - e^{-0.895P})$	?	0.06
Calanus agulhensis (C6♀)	$0.180\ (1 - e^{-0.150P})$	?	0.38
Calanus finmarchicus (C6♀)	$0.057/[1 + e^{40.4\text{-}10.8R}]$	3–5	0.725
Calanus pacificus (C6♀)	0.00102K − 0.0025 (for K <110) 0.1097 (for K > 110)	—	0.85
Calanus pacificus (C6♀)	0.00086L − 0.012 (for L <140) 0.1084 (for L > 140)	—	0.58
Calanus pacificus (*Copepodites*)	$[44.19\ e^{(-0.00774\ DW)}\ (1 - e^{-[1.200 - 2.622\ (log\ (log\ DW))][N - 0.249\ e^{(0.0118\ DW)}]})]/100$	*15.5*	—
Calanus pacificus (*Copepodites*)	$[34.45\ e^{(-0.00641\ DW)}\ (1 - e^{-[1.444 - 3.425\ (log\ (log\ DW))][N - 0.237\ e^{(0.00918\ DW)}]})]/100$	*12.0*	—
Calanus pacificus (*Copepodites*)	$[19.50\ e^{(-0.00326\ DW)}\ (1 - e^{-[2.549\ -\ 5.369\ (log\ (log\ DW))][N - 0.230\ e^{(0.00725\ DW)}]})]/100$	*8.0*	—
Calanus sinicus (C6♀)	$-0.013 + 14.7\ (1 - e^{-0.0038B})$	11.5–15.1	0.38
Calanus sinicus (C6♀)	$0.003 + 0.14\ (1 - e^{-1.00C})$	11.5–15.1	0.69
Calanus sinicus (C6♀)	$0.006 + 0.099\ (1 - e^{-4.19D})$	11.5–15.1	0.67
Calanus sinicus (C6♀)	$-0.005 + 0.10\ (1 - e^{-571E})$	11.5–15.1	0.22
Calanus sinicus (C6♀)	0.13 − 0.085F	11.5–15.1	0.40
Calanus sinicus (C6♀)	$-0.005 + 0.080\ (1 - e^{-0.50B})$	16.8–21.5	0.29
Calanus sinicus (C6♀)	$-0.007 + 0.079\ (1 - e^{-1.39C})$	16.8–21.5	0.50
Calanus sinicus (C6♀)	$-0.009 + 0.073\ (1 - e^{-4.61D})$	16.8–21.5	0.46
Calanus sinicus (C6♀)	$0.001 + 0.071\ (1 - e^{-2.36E})$	16.8–21.5	0.45
Centropages abdominalis (C6♀)	0.330 ln T + 0.125 ln Q − 0.678	8.9–19.7	0.42
Centropages brachiatus (C6♀)	$0.257\ (1 - e^{-0.475P})$	?	0.09
Centropages typicus (C6♀)	$0.12\ (1 - e^{-2.6V})$	11.9–14.2	0.24
Centropages typicus (C6♀)	$0.13\ (1 - e^{-9.8W})$	11.9–14.2	0.38
Nannocalanus minor (C6♀)	$0.253\ (1 - e^{-0.662F})$	?	0.31
Paracalanus sp. (C6♀)	$0.0225 + 0.276\ (1 - e^{-1.279J})$	17.5¶	0.44
Paracalanus sp. (C6♀)	−0.0140 + 0.0575J	17.5¶	0.35
Paracalanus sp. (C6♀)	$0.0589 + 0.320\ (1 - e^{-0.527J})$	17.5¶	0.26
Paracalnus sp. (C6♀)	−0.0125 + 0.0613J	17.5¶	0.55

Table 1. Extended.

p	Location	Period	Source
—	**Onagawa Bay, Japan**	**Sep 77**	**Uye (1981)†**
—	**Onagawa Bay, Japan**	**Sep 77**	**Uye (1981)†**
—	**East Lagoon, U.S.A.**	**May 91**	**Ambler (1986)**
—	**East Lagoon, U.S.A.**	**May 91**	**Ambler (1986)**
—	**East Lagoon, U.S.A.**	**Sep 91**	**Ambler (1986)**
	East Lagoon, U.S.A.	**Nov 91**	**Ambler (1986)**
—	**East Lagoon, U.S.A.**	**Apr–Nov 91**	**Ambler (1986)‡**
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1998)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1998)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1998)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1998)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1998)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1998)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	Malangen Fjord, Norway	Mar–May 89	Diel and Tande (1992)§
—	Puget Sound, U.S.A.	78 and 79	Runge (1985)
—	Puget Sound, U.S.A.	78 and 79	Runge (1985)
—	*Laboratory experiments*	—	*Vidal* (*1980*)
—	*Laboratory experiments*	—	*Vidal* (*1980*)
—	*Laboratory experiments*	—	*Vidal* (*1980*)
—	Inland Sea of Japan	Apr 94	Uye and Murase (1997)
—	Inland Sea of Japan	Apr 94	Uye and Murase (1997)
—	Inland Sea of Japan	Apr 94	Uye and Murase (1997)
—	Inland Sea of Japan	Apr 94	Uye and Murase (1997)
—	Inland Sea of Japan	Apr 94	Uye and Murase (1997)
—	Inland Sea of Japan	Jun 94 and 95	Uye and Murase (1997)
—	Inland Sea of Japan	Jun 94 and 95	Uye and Murase (1997)
—	Inland Sea of Japan	Jun 94 and 95	Uye and Murase (1997)
—	Inland Sea of Japan	Jun 94 and 95	Uye and Murase (1997)
<0.05	Fukuyama Harbor, Japan	Nov 86–Nov 87	Liang et al. (1994)‖
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	NW Mediterranean	Mar 99 and Jan–Feb 00	Calbet et al. (2002)
—	NW Mediterranean	Mar 99 and Jan–Feb 00	Calbet et al. (2002)
—	S. Benguela, South Africa	Sep–Mar 93/94 and 94/95	Richardson and Verheye (1999)
—	Inland Sea of Japan	Jun 85	Uye and Shibuno (1992)
—	Inland Sea of Japan	Dec 85	Uye and Shibuno (1992)
—	Inland Sea of Japan	May 86	Uye and Shibuno (1992)
—	Inland Sea of Japan	Dec 86	Uye and Shibuno (1992)

Table 1. Continued.

Species (stage)	Relationship: weight-specific fecundity/ growth (d^{-1})	Temperature (T, °C)	r^2
Paracalnus sp. (C6♀)	$-17.84 + 18.24\ (1 - e^{-3.7675})$	17.5¶	0.56
Paracalnus sp. (C6♀)	$0.0482 + 0.112J$	17.5¶	0.71
Paracalnus sp. (C6♀)	$0.163 + 0.176\ (1 - e^{-0.256J})$	17.5¶	0.17
Paracalnus sp. (C6♀)	$0.0251 + 0.200\ (1 - e^{-0.530J})$	17.5¶	0.34
Paracalnus sp. (C6♀)	$0.078 + 0.184\ (1 - e^{-0.444J})$	17.5¶	0.25
Paracalnus sp. (C6♀)	$10^{(-4.814 + 0.205T - 0.025J)}$	?	0.88
Mixed (C6♀)	$0.081 \ln (G) - 0.064 \ln (AFDW) + 0.479$	28	0.6
Mixed (C6♀)	$-0.074H + 0.008\ (T \times H) - 0.0172$	~13–29	0.55
Mixed (C6♀)	$-0.195\tau - 0.087H + 0.009(T \times H) - 0.009H^2 - 0.0001\ (T \times H^2) + 1.277$	~13–29	0.70
Broadcast spawners (C6♀)	$10^{(-0.6286 + 0.0468(T) - 0.0528(X) + 0.0214(\log CW \times T)}$	~7.5–14	0.0481
Sac spawners (C6♀)	$10^{(-1.9869 - 0.0512(\%) + 0.0298(X))}$	~7.5–14	0.0512
Broadcast and Sac spawners (C6♀)	$10^{(-1.33319 + 0.1864(\log CW) - (1.0130(\log CW \times T)}$	~7.5–14	0.0481

**Resource descriptor annotations*: (A) Chl *a* (μg L^{-1}) <62 μm size fraction in incubations; (B) Chl *a* (μg L^{-1}) > 1 μm size fraction averaged over water column depth; (C) Chl *a* (μg L^{-1}) > 5 μm fraction averaged over water column depth; (D) Chl *a* (μg L^{-1}) > 20 μm averaged over water column depth; (E) Chl *a* (μg L^{-1}) 5–20 μm fraction averaged over water column depth; (F) Chl *a* (μg L^{-1}) 1–5 μm fraction integrated over water column depth; (G) Chl *a* (μg L^{-1}) >2 μm size fraction; (H) Total Chl *a* (μg L^{-1}) at chlorophyll maximum; (J) Total Chl *a* (μg L^{-1}) at 5 m depth; (K) Chl *a* (mg m^{-2}) >5 μm size fraction integrated over 0–30 m; (L) Total Chl *a* (mg m^{-2}) integrated over 0–30 m; (M) Chl *a* (μg L^{-1}) 5–44 μm size fraction; (N) Concentration of *Thalassiosira eccentrica* and *Thalassiosira angstii* (parts per million); (P) Chl *a* (μg L^{-1}) <63 μm size fraction in incubations from fluorescence maximum; (Q) Chl *a* (μg L^{-1}) <148 μm size fraction in incubations; (R) Total Chl *a* (μg L^{-1}) integrated over 0–15 m; (V) Total Chl *a* (μg L^{-1}) integrated over 0–80 m; (W) Chl *a* (μg L^{-1}) >5 μm size fraction integrated over 0–80 m. (X) Chl *a* (μg L^{-1}) at 3 m water depth.

†Only reproductively active females used.

‡U_a is the CN atomic ratio of particles 1-4 μm in size, and S_a is salinity (‰).

§Water of incubation natural, but from different location from that at which the animals were collected.

‖Adult females with dark oocytes in the ovary and oviducts used.

¶Values corrected to 17.5°C to offset the effect of temperature.

#Abnormally low values between 25 Jul and 3 Oct 86 removed by the authors prior to regression analysis.

**Only incubations where females produced eggs included in their equation derivation. Relationship given in original publication incorrect quoted, corrected version supplied by R. Hopcroft (pers. comm.).

††Temperatures are those measured at 1 m depth.

of their environment), and the food environment consisted of a natural assemblage of locally collected water. Our selection criteria excluded all data where copepods were prestarved or when food was supplemented or intentionally altered. We include those studies where prior to incubation the water was screened to remove either larger predators or eggs, but not those where copepods were incubated in filtered waters (e.g., GF/F, GF/C). The data compiled were only derived from copepods collected within the epipelagic zone, i.e., 0–200 m, and hence our results are only applicable over this depth range. Measurements or approximations of the body and egg weights of the growing individuals given in the original paper (or supplied by the authors) were used in preference. In studies where no egg or body weights were given, we used average egg and/or adult carbon weights for the species from Huntley and Lopez (1992), Kiørboe and Sabatini (1995), or other sources (detailed in data appendices—available upon request). When weights were given as dry or ash-free dry weight they were converted to carbon assuming this to be 40% of dry weight (Båmstedt 1986); ash-free dry weight was assumed to be 89% of dry weight (Båmstedt 1986). When possible, juvenile body weight was defined as the geometric mean weight derived from the initial (W_0) and final weight (W_t) over the period growth was measured (i.e., $[\log_{10} W_t + \log_{10} W_0]/2$). Carbon-specific growth rates were used in preference, but if only dry or nitrogen rates were given we assumed equity to carbon-specific rates. The degree to which temperature and growth values were averaged varies between studies. Some are averaged from more than one location and/or time, but the majority are from collections made at a single location and time; when possible we always used the latter.

In the literature different workers use different equations to estimate growth. We standardize here such that juvenile (NI-CV) copepod weight-specific growth (g, d^{-1}) was assumed to be exponential between points and given as

$$g = \frac{\ln W_t - \ln W_0}{t} \tag{1}$$

where W_0 is the weight of the animal at time zero, W_t is the weight of the animal at time t, and t is the time in days. In actuality changes in weight of juveniles over time are seldom followed, but molt rates are applied to mean weights of stages to determine growth rates, and it is generally such rates we rely upon here.

Adult copepod weight-specific fecundity (g, d^{-1}) was assumed to be linear in form, as eggs are shed and not added to the body weight of the female:

$$g = \frac{W_e}{W_a} \div t \tag{2}$$

W_e is the weight of eggs produced over time t (d) and W_a is the adult weight. Fecundity was converted to weight-specific

Table 1. Continued Extended.

p	Location	Period	Source
—	Inland Sea of Japan	apr 89	Uye and Shibuno (1992)
—	Inland Sea of Japan	Jun 89	Uye and Shibuno (1992)
—	Inland Sea of Japan	May 85	Uye and Shibuno (1992)
—	Inland Sea of Japan	Jun 86	Uye and Shibuno (1992)
<0.05	Inland Sea of Japan	Jan–Dec 86	Uye and Shibuno (1992)
<0.05	Fukuyama Harbour, Japan	Jan–Dec 86	Uye and Shibuno (1992)
—	off Jamaica	90–95	Hopcroft and Roff (1998*a*)**
<0.001	Atlantic transect	Mar–Apr 95	Calbet and Agustí (1999)
<0.001	Atlantic transect	Mar–Apr 95	Calbet and Agustí (1999)
<0.0035	Oregon Coast, U.S.A.	Jun 96	Peterson et al. (2002)††
<0.0692	Oregon Coast, U.S.A.	Jun 96	Peterson et al. (2002)††
<0.0035	Oregon Coast, U.S.A.	Jun 96	Peterson et al. (2002)††

fecundity rates using the egg and adult weights and assuming egg output represented total growth of the adult female. We appreciate that such an assumption does have important errors (Hirst and McKinnon 2001), but unfortunately these are not possible to correct for in the current literature. There is no evidence as yet that these errors are systematic in causing underestimation or overestimation of weight-specific fecundity, however.

For broadcast spawning copepods we use only data collected using the incubation approach detailed above. For the sac-spawning copepods we use results from the incubation approach (e.g., Calbet and Agustí 1999) but also include the egg-ratio method. In this method weight-specific fecundity is derived from the egg to adult female abundance ratio (E_a/F_a), the hatch rate of the eggs (HR, d^{-1}), and the weight of individual eggs (E_w) and females (F_w) (e.g., Nielsen and Sabatini 1996):

$$g = \frac{E_a}{F_a} \times HR \times \frac{E_w}{F_w} \quad (3)$$

Sometimes egg hatch or egg sac production rates have been determined on animals collected at a single temperature, which are then incubated in a range of temperatures. The resultant equations are then applied to seasonal data of in situ temperature and egg–adult abundance (e.g., Uye and Sano 1995). Similarly, relationships of hatching rate and temperature derived in one location are applied to research on the same species but at different times or locations (e.g., Sabatini and Kiørboe 1994). We include such measurements, although we appreciate this may not be the ideal approach since it could cause some biases. No results from the egg-ratio method were included for broadcasting species because a rapid loss of free eggs can occur in the natural environment (Peterson and Kimmerer 1994; Hirst and Kiørboe 2002), potentially resulting in a gross underestimation of weight-specific fecundity. Studies on fecundity that preselected reproductively mature females were not included in the data set, unless values could be adjusted to account for all females.

To be included in our analyses, each growth or fecundity rate required a food-proxy measurement in order to characterize the food environment in which the copepods were being incubated. Initially we included data where any food measure had been made, e.g., POC, particulate organic nitrogen (PON), microplankton counts, and Chl *a* (Table 2). This entire set is used to explore the role of temperature and body size (Tables 3 and 4, Figs. 1 and 2); however, when we then explore the role of food we just consider the subset that is total Chl *a*. The others may as yet prove to be better approximations of food but are too small in number to allow the examination of pattern. The methods used to ascribe a Chl *a* measurement to the fecundity or growth rate varied. We used Chl *a* measurements on the water used to fill the incubation vessel by preference (e.g., Uye and Shibuno 1992), but in the majority of cases we took values from the Chl *a* profiles at the depth incubation water was collected (e.g., Peterson and Kimmerer 1994; Jónasdóttir et al. 1995; Gómez-Gutiérrez and Peterson 1999). If no Chl *a* measurements were available from the exact depths of incubation water collection, then values from within ~5 m of this were accepted. Food proxies that had been averaged or integrated over depth (e.g., Runge 1985; Shreeve et al. 2002) are not used here to examine patterns with Chl *a*. Rather we chose to use volumetric values; these are generally better related to copepod rates than depth-integrated measurements (Calbet and Agustí 1999). When the fluorescence maxima data were cited but they were not close to the depth of water collection (e.g., Nielsen and Sabatini 1996), we excluded these data too. We define GF/F, GF/C, 0.8-μm millipore, and millipore AA filtration data as measures of total Chl *a*, although GF/F overwhelmingly dominates the data set numerically. GF/C with a pore size ~1.2 μm, and millipore AA and 0.8-μm millipore both with pore sizes of ~0.8 μm should underestimate Chl *a* in comparison to GF/F, with a pore size ~0.7 μm. Under the vast majority of situations this error will be relatively small, but it is variable, and we make no corrections here. We do not actively exclude species known to be entirely carnivorous (e.g., *Candacia* spp.), those that feed by piercing and sucking metazoan prey (e.g., *Corycaeus* spp.), or those associated with aggregates or macroscopic particles (e.g., *Oncaea* spp.). However, each of these is either not present in the data or is represented by only a few points.

Table 2. Summary of the copepod weight-specific fecundity and growth rates (g, d^{-1}) under in situ and food saturated laboratory conditions together with the egg hatch (E, d^{-1}) and development rate (D_iD_f, d^{-1}) data. All weight-specific fecundity/growth data (i.e., all food descriptors) used in the in situ analyses presented in Figs. 1 and 2, and Tables 3 and 4 (for which food is not investigated), after which measures from the total Chl *a* data set are presented. Number of data points are the total excluding zero values, numbers of zero values are given in parentheses.

Data type	Group	No. of data points, n (zero values)	No. of species	Source
In situ weight-specific fecundity/growth:				
All food descriptors	Adult broadcasters	3,081 (298)	59	This study
	Adult sac spawners	452 (33)	21	
	Juvenile broadcaster	716 (24)	15	
	Juvenile sac spawners	227 (0)	10	
Total Chl *a*	Adult broadcasters	1,639 (212)	50	This study
	Adult sac spawners	320 (33)	19	
	Juvenile broadcasters	644 (24)	8	
	Juvenile sac spawners	139 (0)	5	
Food saturated weight-specific fecundity/growth	Adult broadcasters	121 (2)	28	This study
	Adult sac spawners	21 (0)	11	
	Juvenile broadcasters	111 (0)	19	
	Juvenile sac spawners	33 (0)	8	
Egg hatch rates	Adult broadcasters	183	34	This study
	Adult sac spawners	173	27	
In situ development rates	Adult broadcasters	107	~19	Hirst and Kiørboe (2002)
	Adult sac spawners	46	~12	
Food saturated development rate	Adult broadcasters	48	16	Adapted from Peterson (2001)
	Adult sac spawners	28	9	

In situ weight-specific fecundity and growth—Analyses and statistical treatment: Species were divided on the basis of whether they represented sac or broadcast spawning species and into adults or juveniles. Regressions between both $\log_e$ weight-specific fecundity and $\log_e$ weight-specific growth to temperature were used to derive Q_{10} values, and the results are given in Table 3 and Fig. 1. To explore the role of body mass, rates of weight-specific fecundity and

Table 3. Relationships between $\log_e$ weight-specific fecundity and growth (g, d^{-1}), egg hatch (E, d^{-1}), and development rates (D_iD_f, d^{-1}) versus temperature (T, °C), *see Figs. 1 and 6.* Q_{10} correction factor derived from the slope as $Q_{10} = e^{(10\times\text{slope})}$. Number of data points are the total on which regressions were performed (i.e., excluding zero values). Given in parentheses are the number of zero values that had to be excluded prior to the regression analysis.

Group	No. of data points, n (zero values)	Temperature range (T, °C)	$\log_e V = a + b[T]$ Intercept (a)	Slope (b)	r^2	p	Q_{10}
In situ weight-specific fecundity/growth ($V = g$, d^{-1})							
Adult broadcasters	3,081 (298)	−2.3–29.4	−3.751	0.0463	0.033	<0.001	1.59
Adult sac spawners	452 (33)	3.0–30.1	−3.367	0.0359	0.057	<0.01	1.43
Juvenile broadcasters	716 (24)	7.6–28.2	−2.898	0.0786	0.139	<0.001	2.19
Juvenile sac spawners	227 (0)	6.5–28.2	−3.453	0.0881	0.506	<0.001	2.41
Food saturated weight-specific fecundity/growth ($V = g$, d^{-1})							
Adult broadcasters	121 (2)	−1.5–30.0	−3.337	0.0994	0.404	<0.001	2.70
Adult sac spawners	21 (0)	1.3–23.8	−4.328	0.1381	0.383	<0.005	3.98
Juvenile broadcasters	111 (0)	3.0–30.0	−2.323	0.0623	0.256	<0.001	1.86
Juvenile sac spawners	33 (0)	3.0–25.0	−2.514	0.0605	0.477	<0.001	1.83
Egg hatch rate ($V = E$, d^{-1})							
Broadcasters	183	0.0–29.8	−1.822	0.0895	0.728	<0.001	2.45
Sac spawners	173	−1.0–34.0	−2.433	0.0877	0.826	<0.001	2.40
In situ development rate ($V = D_1$, d^{-1})							
Broadcasters + sac spawners	153	0.0–29.2	−4.438	0.0755	0.666	<0.001	2.13
Food saturated development rate ($V = D_f$, d^{-1})							
Broadcasters + sac spawners	76	5.0–28.5	−4.361	0.0788	0.710	<0.001	2.20

Table 4. Relationships between $\log_{10}$ weight-specific fecundity/growth (g, d^{-1}) under both in situ and food saturated laboratory conditions to $\log_{10}$ body weight (BW, μgC/ind^{-1}), $\log_{10}$ in situ development rates (D_i, d^{-1}) to $\log_{10}$ adult body weights, and $\log_{10}$ egg hatch rates (E, d^{-1}) to $\log_{10}$ egg weight (BW, μgC ind^{-1}). All data corrected to 15°C using the group-specific Q_{10} values given in Table 3 prior to analyses. Number of data points are the total on which regressions were performed (i.e., excluding zero values). Given in parentheses are the number of zero values that had to be excluded prior to the regression analysis.

Group	No. of data points, n (zero values)	Body weight range (BW, μgC ind.$^{-1}$)	$\log_{10} V = a + b[\log_{10}$ BW] Intercept (a)	Slope (b)	r^2	p
In situ weight-specific fecundity/growth ($V = g$, d^{-1})						
Adult broadcasters	3,081 (298)	0.380–3,620	−1.003	−0.251	0.055	<0.001
Adult sac spawners	452 (33)	0.199–119.23	−1.254	0.171	0.052	<0.001
Juvenile broadcasters	716 (24)	0.036–72.10	−0.679	−0.136	0.087	<0.001
Juvenile sac spawners	227 (0)	0.017–39.18	−0.942	−0.031	0.006	>0.05ns
Food saturated weight-specific fecundity/growth ($V = g$, d^{-1})						
Adult broadcasters	121 (2)	1.5–356.0	−0.609	−0.197	0.154	<0.001
Adult sac spawners	21 (0)	0.924–722.0	−0.656	−0.419	0.379	<0.005
Juvenile broadcasters	105 (0)	0.046–100.0	−0.583	−0.088	0.083	<0.005
Juvenile sac spawners	31 (0)	0.089–4.0	−0.681	0.046	0.022	>0.20ns
Egg hatch rate ($V = E$, d^{-1})						
Broadcasters	167	0.022–0.924	−0.0709	0.147	0.170	<0.001
Sac spawners	165	0.002–0.170	−0.339	0.0998	0.147	<0.001
In situ development rate ($V = D_i$, d^{-1})						
Broadcasters + sac spawners	151	0.24–760	−1.351	−0.121	0.136	<0.001

growth were corrected to 15°C using these group-specific Q_{10} values: 1.59 and 2.20 for broadcast adults and juveniles, 1.43 and 2.41 for sac-spawning adults and juveniles, respectively. The temperature-corrected rates were then $\log_{10}$ transformed and regressed against $\log_{10}$ body weight (*see Fig. 2 and Table 4*), as is the common practice in examination of scaling.

Michaelis–Menten relationships were determined in order to examine patterns between weight-specific fecundity/growth and Chl *a* concentration for adult and juvenile broadcast and sac spawners. All rates were first corrected to 15°C and then to 10 μg C ind^{-1} using the appropriate Q_{10} and scaling slopes (Fig. 3 and Table 5). Since *Calanus* spp. and *Oithona* spp. contributed a large number of the data points within the adult broadcast and sac spawner data sets, relationships were also derived for these excluding these genera. To examine differences in the variability of juvenile weight-specific growth and adult weight-specific fecundity, we use these same corrected rates and derive mean and standard deviation (SD) including the zero values in each of the data sets (Fig. 4).

Michaelis–Menten relationships were derived for individual genera when there were sufficient data (sufficiency was defined as $n > 95$). Data were corrected to 15°C but no correction for body weight was made in this case (Fig. 5 and Table 5). Although for adult relationships six genera fell into this category, only one juvenile genus had sufficient data points, namely *Calanus* spp.

To examine the relationship between the weight-specific fecundity/growth and the three factors—temperature, body weight, and Chl *a*—we used backward step-wise regression. The dependent variable was $\log_{10}$ weight-specific fecundity or growth (g, d^{-1}), and the independent variables were temperature (T, °C), $\log_{10}$ body weight (BW, μg C ind^{-1}), and $\log_{10}$ Chl *a* concentration (C_a, μg Chl *a* L^{-1}). F to enter was set at 4.0, and F to remove at 3.9. Where no independent variables were removed, a multiple linear regression (SigmaStat Package, SPSS) was produced of the form $\log_{10} g = a[T] + b[\log_{10}\text{BW}] + c[\log_{10} C_a] + d$. If an independent variable did not add significantly to the prediction it was excluded, and the regression was completed using the remaining variables. We chose to $\log_{10}$ transform the C_a term, since this approximately linearizes the data. It is a mathematical impossibility to perfectly linearize a Michaelis–Menten function when the dependent (g) term is logged (as deemed appropriate in relating to body weight and temperature). Results are given in Table 6 together with R^2 values and significance levels.

Food saturated weight-specific fecundity and growth—Data compilation: In order to examine the degree to which in situ rates were food limited at different temperatures and body sizes, we compiled growth and fecundity rates under laboratory conditions where food was supplied in what was believed to be excess. We began by reexamining the original data sources compiled by Kiørboe and Sabatini (1995), but, unlike their analysis, our analysis includes measurements across a wide range of temperatures. Additional data from other published sources were also added here. We compiled mean maximum rates rather than absolute individual maximum. Measures where wild animals were collected, given excess food, and fecundity or growth was measured shortly afterward were not included (e.g., Saiz et al. 1999). Copepods can take some time to acclimate to a change in food, and using such values can underestimate the food saturated rates. Results are presented in Figs. 6 and 7, and Tables 3 and 4.

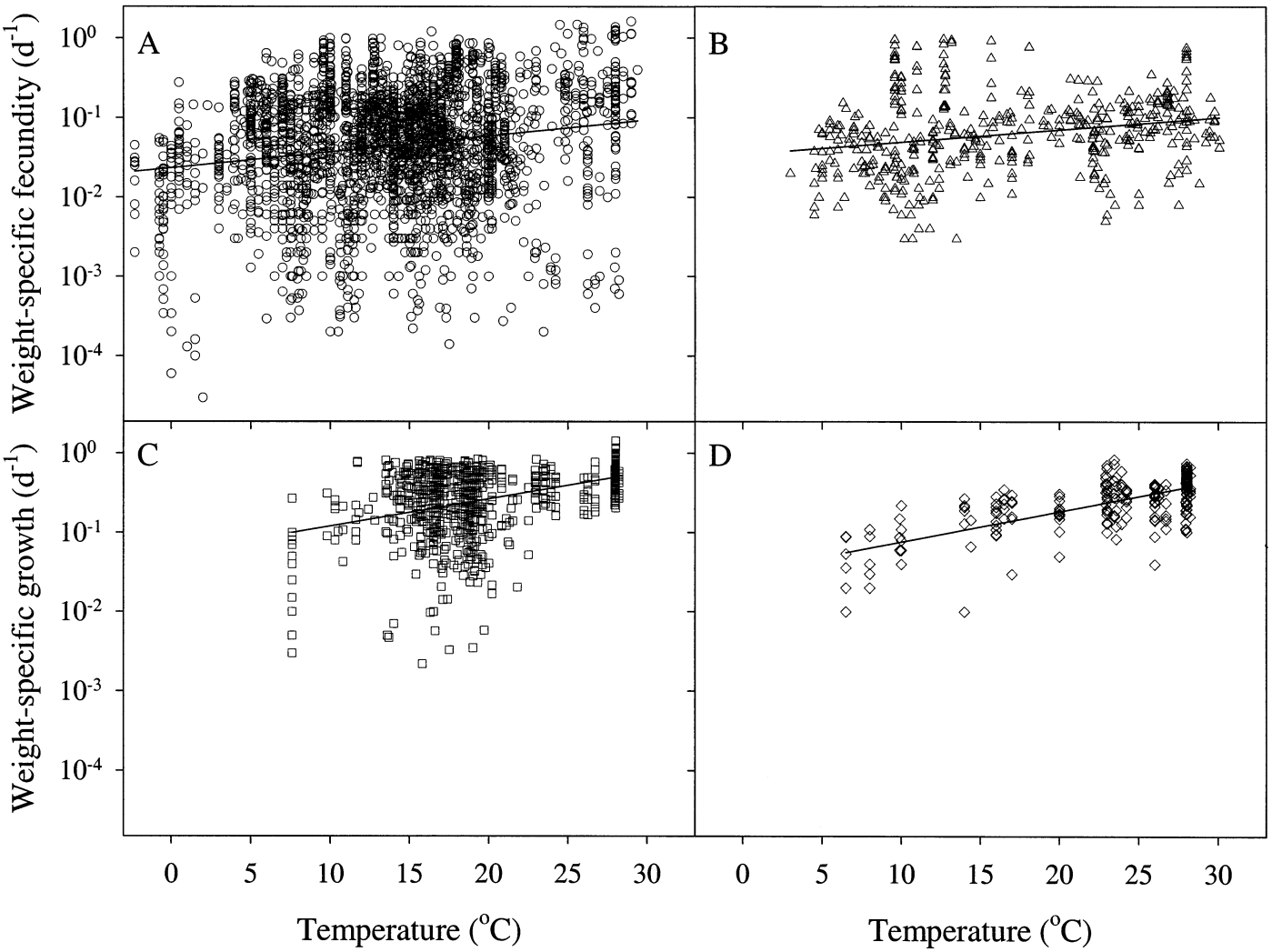

Fig. 1. Weight-specific fecundity and growth rates of copepods as a function of temperature in (A) adult broadcasters, (B) adult sac spawners, (C) juvenile broadcast spawners, and (D) juvenile sac spawners. Solid lines describe regressions that are significant. Results from these analyses are given in Table 3.

Laboratory food saturated rates were compared with their in situ equivalents using analysis of covariance (ANCOVA; SPSS Package). First slopes were examine for being parallel, and if they were, than intercepts they were then tested for significant difference; these results are presented in Table 7.

Egg hatch and development rates—Egg hatch times of broadcast and sac-spawning copepods were taken from the published literature together with the temperatures at which they were incubated. Egg carbon weights were taken from the original study, but if not present then we relied upon other sources (e.g., Huntley and Lopez 1992; Kiørboe and Sabatini 1995) or we derived weights from egg diameter by assuming egg carbon content to be 0.14×10^{-6} μg C μm^{-3} (Kiørboe et al. 1985; Huntley and Lopez 1992). Although various definitions have been applied (e.g., mean hatch time, time to 50% hatch), we made no distinction here, and hatch rates were derived as the reciprocal of the hatch time. The egg hatch rates are believed to be generally unaffected by food availability. They were therefore compiled as an aid in examining life-history rates in relation to temperature, when food is not limiting. All data sets are available from the authors upon request.

Copepod field development times (egg laying to molt to adulthood) were taken from Hirst and Kiørboe (2002), and rates were derived as the reciprocal of these times. Food saturated laboratory development rates were taken from table 1 of Peterson (2001), but we include here only the brackish and marine data. Since their rates are postembryonic development times and exclude the egg hatch time, we add an estimate of this to each of their values. These were predicted using the egg hatch to temperature regressions for broadcast and sac spawners derived here (Table 4).

As with weight-specific fecundity and growth rates, comparisons between in situ and laboratory food saturated rates were made using ANCOVA analysis, while for egg hatch rates we compared the broadcaster rates with those for sac spawners. First, slopes were examined to see if they were

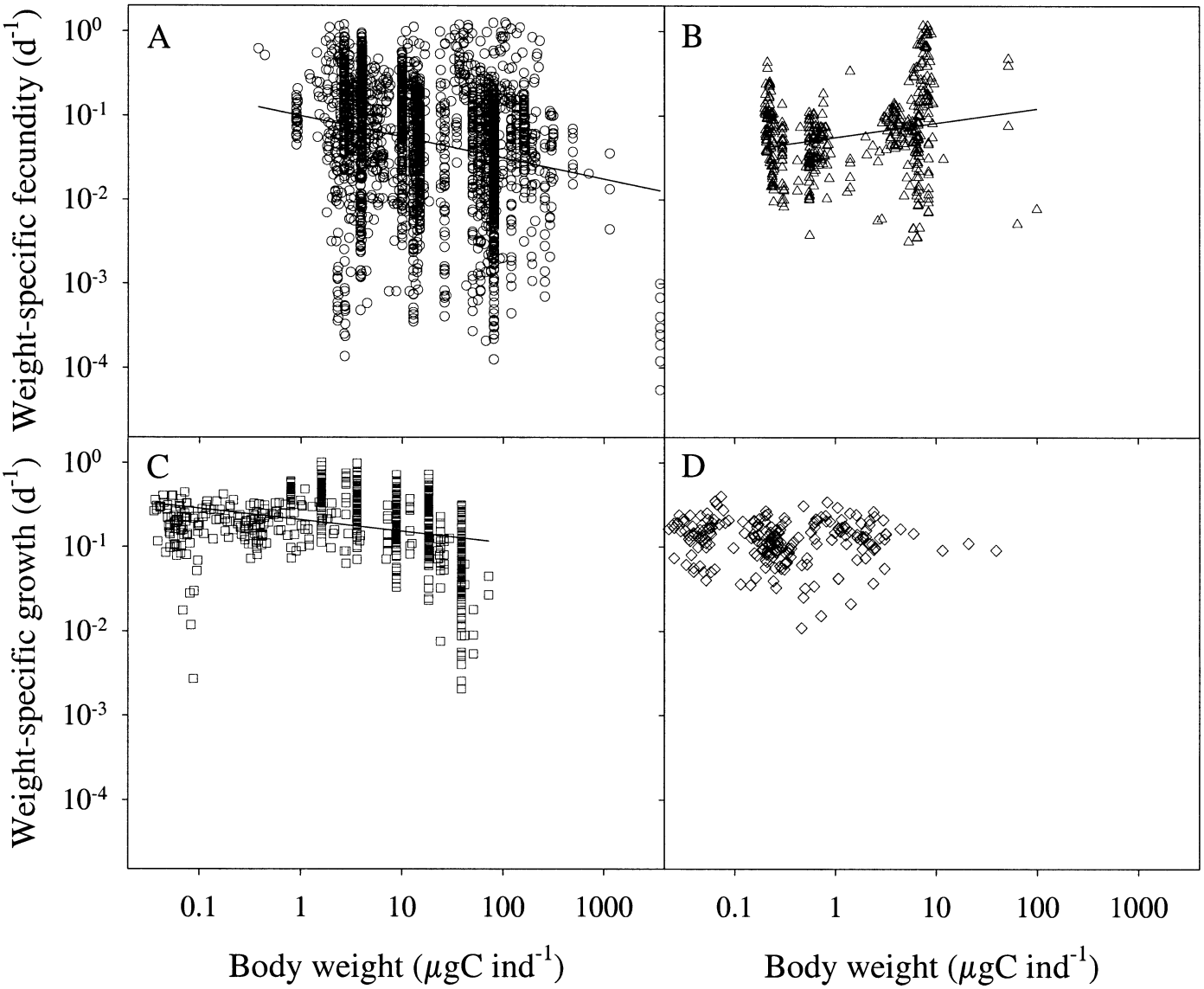

Fig. 2. Weight-specific fecundity and growth rates of copepods as a function of body size in (A) adult broadcasters, (B) adult sac spawners, (C) juvenile broadcasters, and (D) juvenile sac spawners. All weight-specific fecundity/growth rates corrected to 15°C using group-specific Q_{10} values. Solid lines describe regressions that are significant. Results from these analyses are given in Table 4.

parallel, and if they were intercepts were then tested for significant difference. We compared rates with respect to an *x*-axis of both temperature and $\log_{10}$ body weight (Table 7).

Results

In situ weight-specific fecundity and growth—The data set contains 4,831 weight-specific fecundity and growth measurements in total. The measurements are from ~88 copepod species within 29 genera. Body sizes of adults range from 0.199 to 3,260 μg C ind^{-1}, and those of juveniles range from 0.017 to 72.1 μg C ind^{-1}. The entire data set includes measurements made in environments from the tropics to the poles, with temperature ranging from −2.3 to 30.6°C. This lowest value is from the work of Smith (1990) in a study of the Fram Strait, Greenland Sea, the temperature being described as close to the freezing point at the prevailing salinities. Estuarine, coastal upwelling through to oligotrophic open ocean data were included, and total Chl *a* concentrations varied by more than four orders of magnitude, from 0.016 to 321.6 μg Chl *a* L^{-1}. Table 2 summarizes the data set and food-proxy types. The food proxy total Chl *a* dominated the entire data set, representing 3,011 of the total 4,831 measurements.

Weight-specific fecundity of adults and growth of juveniles increases significantly with temperature for both broadcast and sac-spawning copepods ($p < 0.01$ to <0.001) (*see Fig. 1 and Table 3*). The relationships between weight-specific fecundity and temperature are very similar for adult broadcast and sac spawners with respect to intercepts and slopes, with Q_{10} values of 1.59 and 1.43, respectively. These adult Q_{10} values are much lower than those in juvenile broad-

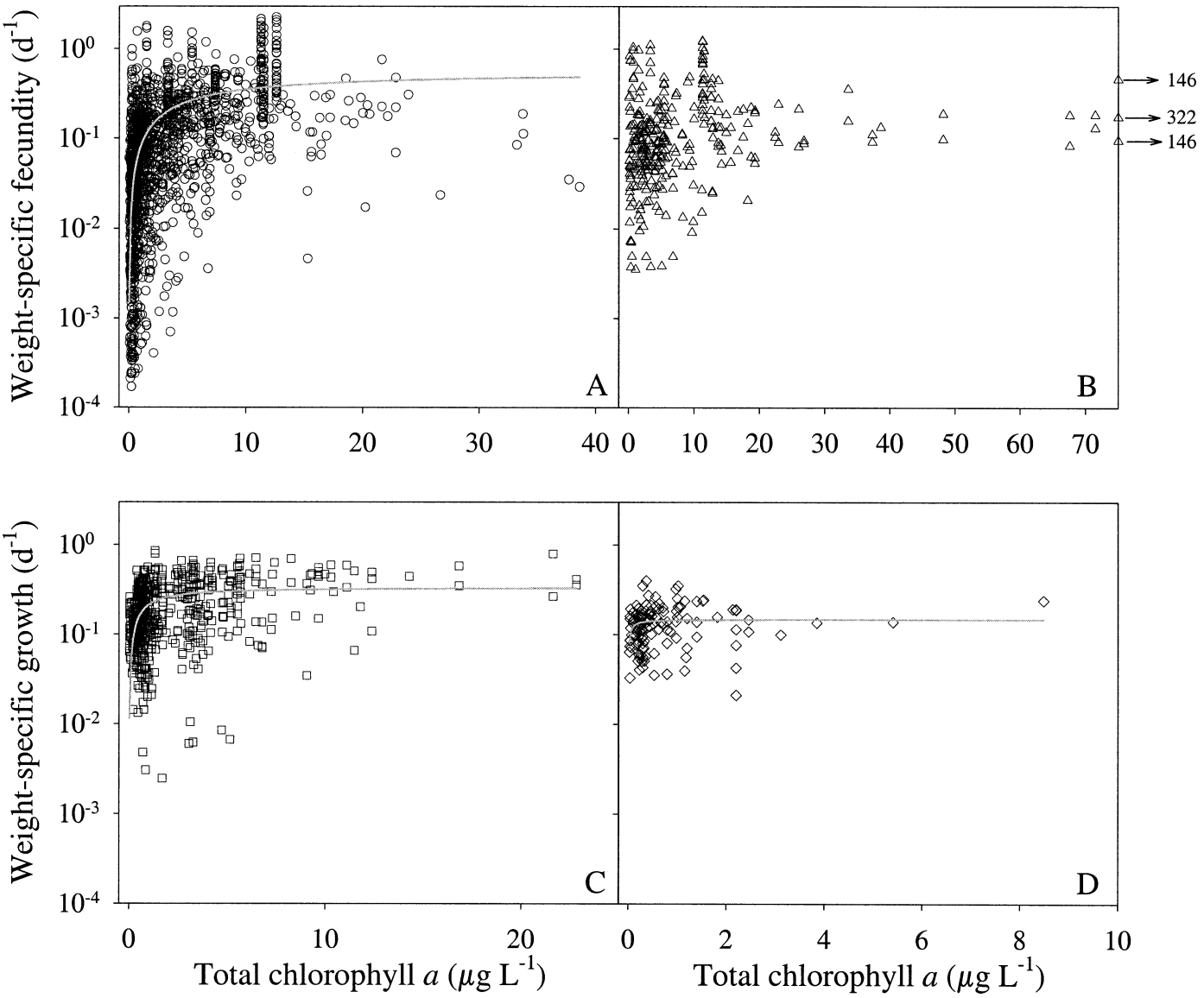

Fig. 3. Michaelis–Menten relationships between in situ weight-specific fecundity/growth rates (g, d^{-1}) and Chl *a* concentration (C_a, μg Chl *a* L^{-1}). (A) Adult broadcasters, (B) adult sac spawners, (C) juvenile broadcasters, and (D) juvenile sac spawners. All values first corrected to 15°C and then to a body weight of 10 μg C ind^{-1} using group-specific values. Note change in scales. Results from these analyses are given in Table 5.

cast and sac spawners, which are 2.19 and 2.41, respectively. The results in Fig. 2 and Table 4 show that weight-specific fecundity of adult broadcasters scales negatively with body weight ($p < 0.001$). The scaling of juvenile broadcaster growth is also significant and negative ($p < 0.001$), but the slope is weaker than for the adults. Adult sac spawners show a significant ($p < 0.001$) and positive relationship, whereas their juveniles show no evidence of scaling ($p > 0.05$).

The results of the Michaelis–Menten plots for the copepod data corrected to 15°C and 10 μg C ind^{-1} are shown in Fig. 3 and Table 5. Broadcaster adults have the highest g_{max} of 0.558 d^{-1}, but with a K_m of 5.94 μg Chl *a* L^{-1} they also require the highest Chl *a* concentration to achieve half-saturation. For sac-spawning adults, the relationship is not significant ($p = 0.441$). Juvenile broadcasters have a g_{max} of 0.335 d^{-1}, which is slightly lower than their adults, but the juvenile K_m is an order of magnitude lower than their adults at just 0.59 μg Chl *a* L^{-1}. A similar pattern is observed in the single case for which we can compare within a genus, namely *Calanus*, in which the adults require 20 times the Chl *a* concentration to achieve half-saturation of their weight-specific fecundity than juveniles do for their growth. Sac-spawner juveniles have both the lowest g_{max}, at just 0.148 d^{-1}, and the lowest K_m, at 0.02 μg Chl *a* L^{-1}. Genera-specific results are presented in Table 5 and Fig. 5. The g_{max} values for the broadcasting genera range between 0.303 and 0.605 d^{-1}. Adult *Calanus* has the highest K_m values at 10.71 μg Chl *a* L^{-1}; it also has a much higher mean body weight than the other genera at 121.4 μg C ind^{-1}. The lowest K_m value for the adults is in *Paracalanus* at 0.85 μg Chl *a* L^{-1}.

Table 5. Michaelis–Menten relationships between weight-specific fecundity and growth (g, d^{-1}) and chl a concentration (C_a, μg Chl a L^{-1}) for all the groups, and genera specific relationships where $n > 95$. Weight-specific fecundity/growth rates corrected to 15°C using group-specific Q_{10} values.

Group	No. of data points, n	No. of species	Mean body weight (BW, μg C ind.$^{-1}$)	Temperature range (°C)	Chl a range (C_a, μg Chl a L^{-1})	$g = C_a\,[g_{max}]/(C_a + K_m)$		r^2	p
						g_{max} (SE)	K_m (SE)		
Adult broadcasters	1,851	50	10*	0.0–29.0	0.016–38.62	0.558 (0.045)	5.94 (0.97)	0.210	<0.0001
Adult sac spawners	353	19	10*	3.0–30.1	0.069–321.6	0.170 (0.015)	0.12 (0.13)	0.002	0.441ns
Juvenile broadcasters	668	8	10*	9.8–28.2	0.021–22.82	0.335 (0.015)	0.59 (0.09)	0.148	<0.0001
Juvenile sac spawners	139	5	Uncorrected	6.5–28.2	0.027–8.49	0.148 (0.008)	0.02 (0.01)	0.034	0.030
Adult broadcasters (without *Calanus* spp.)	944	42	10*	0.0–29.0	0.061–38.62	0.292 (0.016)	2.379 (0.39	0.244	<0.0001
Adult sac spawners (without *Oithona* spp.)	213	12	10*	3.0–28.2	0.128–146.0	0.209 (0.029)	0.491 (0.44)	0.016	0.062ns
Broadcaster genera									
Adult *Acartia* spp.	366	12	4.99	3.0–29.0	0.140–33.75	0.478 (0.044)	2.75 (0.69)	0.250	<0.0001
Adult *Calanus* spp.	907	9	121.43	0.0–25.0	0.016–33.79	0.430 (0.076)	10.71 (3.18)	0.204	<0.0001
Adult *Centropages* spp.	192	5	20.19	3.0–28.0	0.140–33.24	0.605 (0.083)	4.60 (1.56)	0.303	<0.0001
Adult *Paracalanus* spp.	101	3	2.80	8.0–28.2	0.161–38.62	0.303 (0.057)	0.85 (0.54)	0.100	0.0012
Juvenile *Calanus* spp.	472	1	15.89	9.8–22.5	0.180–22.50	0.379 (0.022)	0.54 (0.12)	0.092	<0.0001
Sac spawner genera									
Adult *Pseudocalanus* spp.	98	3	7.99	3.0–18.1	0.140–12.60	0.375 (0.061)	0.83 (0.67)	0.055	0.020
Adult *Oithona* spp.	140	7	0.32	8.9–30.06	0.069–321.6	0.071 (0.006)	−0.045 (0.01)	0.044	0.012

*Values corrected to a body weight of 10 μg C ind^{-1} using slopes given in Table 4 when these were significant. In these relationships no zero values had to be removed.

While the g_{max} values for the adult broadcasters do not rank according to the genus' body weight, the K_m values do, progressively increasing with increasing body weight in the four genera. The sac spawner *Pseudocalanus* has a similar g_{max} (0.375) and K_m (0.83) to the broadcaster *Paracalanus*, although it is larger in body weight at 8.0 μg C ind^{-1}. *Oithona* is found to have a negative K_m; this is the result of the presence of some high weight-specific fecundity values at very low Chl *a* values in a tropical study. If these few data points are excluded the relationship has the more typical form.

Backward step-wise regression reveals that weight-specific fecundity of broadcasters and sac spawners and growth in juvenile broadcasters are found to be dependent upon all three of the variables, temperature, Chl *a*, and body weight, when tested using Table 6. In only the sac-spawning juveniles is Chl *a* not found to add to the prediction and hence not included in the relationship.

Food saturated weight-specific fecundity and growth—We include 288 measurements from 50 species, ranging in temperature from −1.5°C to 30.0°C (Table 2). Weight-specific fecundity and growth are significantly related to temperature; adults have Q_{10} values of 2.70 and 3.98 for broadcast and sac spawners, respectively, while for juveniles these are slightly lower at 1.86 and 1.83 (Table 3). Rates under laboratory food saturation and in situ are compared as a function of temperature (Fig. 6) and body weight ($p < 0.0001$, Fig. 7). Food saturated rates are found to scale negatively and significantly with body size in broadcast adults ($p < 0.001$) and juveniles ($p < 0.005$). Juvenile sac spawners are found to have an insignificant relationship ($p > 0.20$), while for their adults the relationship is negative and significant ($p < 0.005$).

Egg hatch and development rates—A total of 356 egg hatch rates were compiled from 61 species (Table 2). These together with development rates are examined as a function of temperature (Fig. 6, Table 3) and body weight (Fig. 7, Table 4). Egg hatch rates increased significantly with increasing temperature ($p < 0.001$); i.e., hatch times decreased. The slopes for both broadcast and sac spawners are very similar, with Q_{10}s of 2.45 and 2.40, respectively. Intercepts, however, are significantly different (Table 7), and sac spawners have much longer egg hatch times (lower egg hatch rates). We found significant ($p < 0.001$) positive relationships between egg hatch rate and egg weight, suggesting that large eggs hatch in a shorter time than small eggs. We find very large eggs may have very long egg hatch times, these are bracketed in Fig. 7 and not included in the regression for hatch against egg size or the ANCOVA tests. Comparing egg hatch rates against egg weight, we find that broadcasters and sac spawners have parallel slopes but intercepts are significantly different ($p < 0.0001$, Table 7), this coincides with the results from the comparisons of these groups as a function of temperature.

Discussion

Relationships with temperature—Measurements of rate process that are unlimited by food (laboratory food saturated

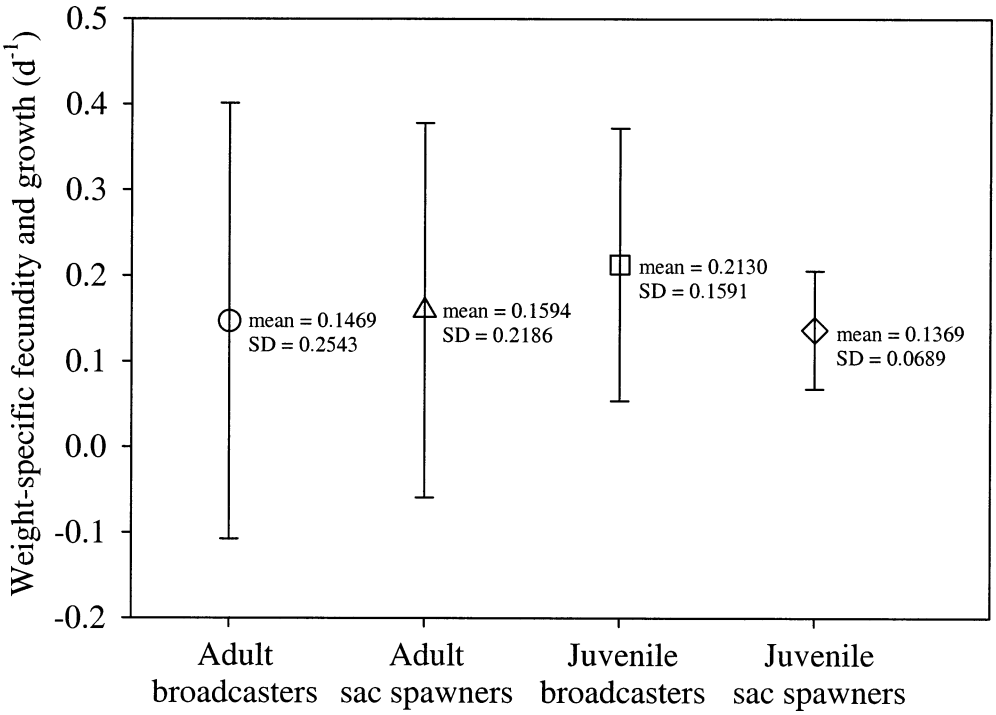

Fig. 4. Mean and ±SD of in situ weight-specific fecundity/growth rates (g, d^{-1}) of adult broadcasters, adult sac spawners, juvenile broadcasters, and juvenile sac spawners. All values first corrected to 15°C and then to a body weight of 10 μg C ind^{-1} using group-specific values; zero values included in the determination of these values.

weight-specific fecundity, weight-specific growth, development, and egg hatch rates) have Q_{10}s that vary between 1.8 and 2.7, the only outlier being sac-spawner weight-specific fecundity at 3.98. This high value may be the result of insufficient data for this group. On average, egg hatch times are a relatively constant proportion of the full in situ development time, irrespective of temperature (Fig. 6), at between 5% and 7% for broadcasters and 9% and 13% for sac spawners (as derived from the regressions over their temperature range). The more rapid egg hatch times of broadcasters compared to sac spawners may result from strong selection pressure to reduce the length of this vulnerable period, since free eggs suffer much higher mortality rates than those attached to the female (Hirst and Kiørboe 2002). Interestingly, the sac-spawned eggs take ~1.9 times longer on average to hatch than broadcast eggs, and this ratio is independent of temperature or egg weight.

In situ growth of juvenile broadcast and sac-spawning copepods shows strong dependence on temperature, with Q_{10} values of 2.19 and 2.41, respectively. These regressions fall below, but close to, those for laboratory food saturated animals (Fig. 6). ANCOVA tests show that for juvenile broadcasters the slopes of in situ rates and food saturated growth rates are parallel, but the intercepts are significant different ($p = 0.001$, Table 7), while for the sac spawners the slopes are not parallel, and therefore intercepts cannot be tested. At 15°C the in situ growth rates are 72% and 59% of food saturated rates in broadcast and sac spawners. Development rates under food saturated and in situ conditions versus temperature are found to have parallel slopes, but intercepts are significantly different ($p = 0.015$), this is in contrast to the findings of Huntley and Lopez (1992), but our data set is larger and more comprehensive. Development rates in the field at 15°C are on average 88% of those at food saturation; the fact that this is closer to food saturation than the juvenile growth rates leads us to suggest that development rates overrepresent faster growing individuals. This may be a result of greater survival of fast-growing individuals (Lopez 1991) and/or simply a consequence of bias in how we measure development (Carlotti and Nival 1991; Hirst and Sheader 1997).

The higher slopes and Q_{10} values for juvenile growth compared to that of adult weight-specific fecundity suggest that agents not limiting juveniles may limit adult fecundity; we return to this topic later. The higher variability in adult weight-specific fecundity when plotted against temperature or body weight (Figs. 1 and 2) in comparison to juvenile growth, and when corrected for these (Fig. 4), suggests that other factors may be critical to adults and less so for juveniles. In addition to food availability, these might include mate limitation, reproductive status, and the proportion of prereproductive and postreproductive individuals. Interclutch periods that are greater than the period of incubation and spawning synchronicity may both erroneously act to inflate the apparent variability in adult weight-specific fecundity (*see* Hirst and McKinnon 2001). Juveniles have fewer body reserves and may die more rapidly than adults when their growth conditions diverge from near maximal; this may ex-

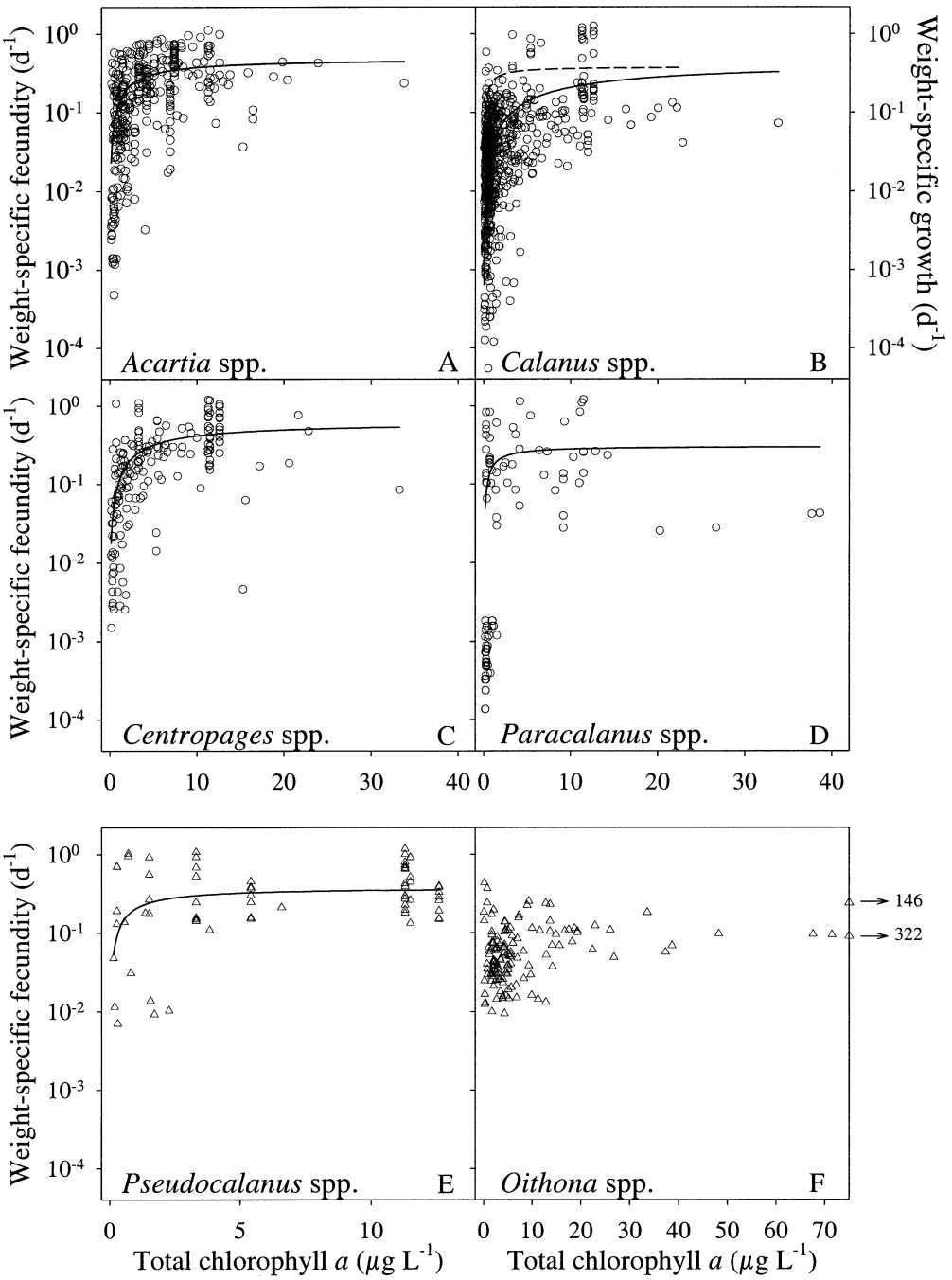

Fig. 5. Michaelis–Menten relationships between in situ weight-specific fecundity (circles for broadcasters, triangles for sac spawners, relationship given by solid lines) and Chl *a* concentration (C_a, μg Chl *a* L^{-1}) for six copepod genera: (A) *Acartia* spp., (B) *Calanus* spp., (C) *Centropages* spp., (D) *Paracalanus* spp., (E) *Pseudocalanus* spp., and (F) *Oithona* spp. In the case of *Calanus* spp. growth relationship for juveniles also plotted (data points not indicated, relationship given by dashed lines) (g, d^{-1}). All individual weight-specific rates first corrected to 15°C using group-specific Q_{10} values, no body weight corrections were made. Results from these analyses are given in Table 5.

plain why slow-growing juveniles are not as commonly found as slow-growing adults and, hence, why they have less variable growth rates. We discuss the topic of how juvenile mortality may act on the rates of growth we observe in more detail later.

Body weight scaling—Food modification: Our findings of increasing egg hatch rates with egg size contradict the findings of Kiørboe and Sabatini (1995), who found no significant scaling; however, they only considered data from 11 and 17 species of sac and broadcaster, respectively. We pre-

Table 6. Results from the regressions relating the dependent variable $\log_{10}$ weight-specific fecundity/growth (g, d^{-1}) to independent variables temperature (T, °C), $\log_{10}$ body weight (BW, μg C ind^{-1}), and total Chl a concentration (C_a, μg Chl a L^{-1}). For those data sets in which an independent variable did not statistically significantly add to prediction this was removed, and those remaining used in the formulation of a multiple linear regression.

Group	Backward stepwise regression	Multiple linear regression $\log_{10} g = a[T] + b[\log_{10} \text{BW}] + c[\log_{10} C_a] + d$						Multiple linear regression $\log_{10} g = a[\text{var. 1}] + b[\text{var. 2}] + c$						
		a	b	c	d	R^2	p	a	b	c	var. 1; var. 2	R^2	p	(n)
							(T; $\log_{10}$ BW; $\log_{10} C_a$)						(var 1; var 2)	
Adults														
Broadcasters	All included	0.0125	−0.230	0.729	−1.348	0.357	<0.001; <0.001; <0.001	—	—	—	—	—	—	(1,639)
Sac spawners	All included	0.0182	0.193	0.195	−1.591	0.113	<0.001; <0.001; <0.001	—	—	—	—	—	—	(320)
Juveniles														
Broadcasters	All included	−0.0143	−0.363	0.135	−0.105	0.392	<0.001; <0.001; <0.001	—	—	—	—	—	—	(644)
Sac spawners	C_a removed	—	—	—	—	—	—	0.0333	−0.163	−1.528	T; $\log_{10}$BW	0.595	<0.001; 0.003	(139)
All data	All included	0.0186	−0.288	0.417	−1.209	0.289	<0.001; <0.001; <0.001	—	—	—	—	—	—	(2,742)

Fig. 6. Rate parameters of marine planktonic copepods versus temperature (T, °C) under in situ and food saturated laboratory conditions. (A) Egg hatch rates (E, d^{-1}) of broadcast (small solid circles) and sac spawners (small solid triangles). Food saturated development rates (D_f, d^{-1}) (large solid circles, broadcasters; large solid triangles, sac spawners), and in situ development rates (D_i, d^{-1}) (large solid circles, broadcasters; large open triangles, sac spawners). (B) Food saturated weight-specific growth (g, d^{-1}) of broadcast (solid squares) and sac-spawner juveniles (solid diamonds). (C) Food saturated weight-specific fecundity (g, d^{-1}) of broadcast (solid circles) and sac-spawner adults (solid triangles). In (B) and (C) in situ relationships given by heavy lines for comparison, broadcasters dashed lines, and sac spawners solid lines.

sent a far more extensive set of data here. Given that egg hatch rate increases with egg size, while full development rate decreases (Fig. 7) and larger animals produce larger eggs (Kiørboe and Sabatini 1995), we can conclude that the proportion of the full development time (egg to adulthood) spent as eggs decreases considerably with increasing body size in the copepods.

Weight-specific fecundity and growth have often been observed to scale negatively with body size in many environment types: tropical waters off Jamaica (Hopcroft and Roff

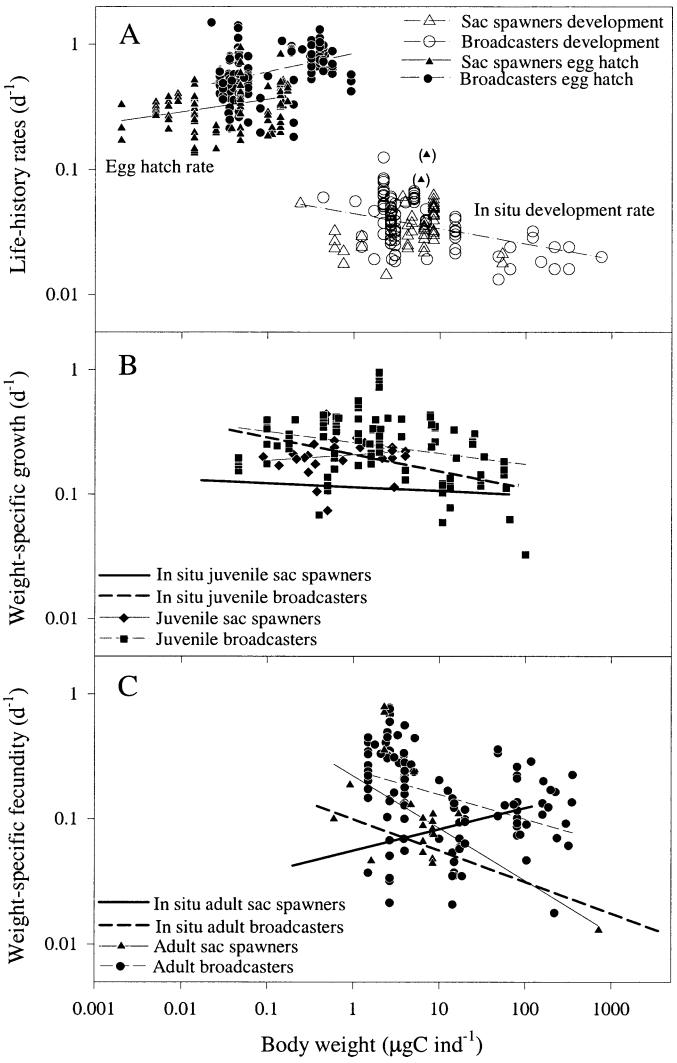

Fig. 7. Rate parameters of marine planktonic copepods versus body weight (BW, μg C ind^{-1}) under in situ and food saturated laboratory conditions, all values are corrected to 15°C using appropriate Q_{10}s. (A) Egg hatch rates (E, d^{-1}) of broadcast (small solid circles) and sac spawners (small solid triangles), body weights are those of the eggs. The two large eggs in brackets not included in regression. In situ development rates (D_i, d^{-1}) (large open circles, broadcasters; large open triangles, sac spawners) and body weights are those of the adults. (B) Food saturated weight-specific growth (g, d^{-1}) of broadcast (solid squares) and sac-spawner juveniles (solid diamonds). (C) Food saturated weight-specific fecundity (g, d^{-1}) of broadcast (solid circles) and sac-spawner adults (solid triangles). In (B) and (C) in situ relationships given by heavy lines for comparison, broadcasters dashed lines, and sac spawners solid lines.

1998*a*,*b*; Hopcroft et al. 1998), northern and southern Benguela upwelling and Angola-Benguela region (Richardson and Verheye 1998, 1999; Richardson et al. 2001), Skagerrak coastal waters (Peterson et al. 1991), and shelf waters off Oregon (Peterson et al. 2002). However, our analysis shows that scaling is negative in broadcast adults and juveniles but lacking in juvenile sac spawners. Scaling may be negative or positive in sac-spawning adults depending on the balance of data and availability of food (*see Fig. 7*). When in situ

Table 7. Results from ANCOVA analysis comparing food saturated and in situ rates for weight-specific fecundity, growth, and development times. Egg hatch rates are compared between broadcast and sac spawners. B = broadcasters, S = Sac spawners, A = Adults, J = Juveniles.

ANCOVA groups				Parallelism of lines significance (p)	ANCOVA significance (p)	
1	2	Relationships	Figure			Conclusion
B	S	$\log_e E$ vs. T	6A	0.729	<0.0001	Slopes parallel, Intercepts significantly different
B+S in situ	B+S food saturated	$\log_e D$ vs. T	6A	0.723	0.015	Slopes parallel, Intercepts significantly different
B	S	$\log_{10} E$ vs. $\log_{10}$ BW	7A	0.134	<0.0001	Slopes parallel, Intercepts significantly different
JB in situ	JB food saturated	$\log_e g$ vs. T	6B	0.356	0.001	Slopes parallel, Intercepts significantly different
JS in situ	JS food saturated	$\log_e g$ vs. T	6B	<0.05	—	Slopes not parallel
JB in situ	JB food saturated	$\log_{10} g$ vs. $\log_{10}$ BW	7B	0.299	0.005	Slopes parallel, Intercepts significantly different
JS in situ	JS food saturated	$\log_{10} g$ vs. $\log_{10}$ BW	7B	0.583	<0.0001	Slopes parallel, Intercepts significantly different
AB in situ	AB food saturated	$\log_e g$ vs. T	6C	0.013	—	Slopes not parallel
AS in situ	AS food saturated	$\log_e g$ vs. T	6C	0.027	—	Slopes not parallel
AB in situ	AB food saturated	$\log_{10} g$ vs. $\log_{10}$ BW	7C	0.583	<0.0001	Slopes parallel, Intercepts significantly different
AS in situ	AS food saturated	$\log_{10} g$ vs. $\log_{10}$ BW	7C	0.01	—	Slopes not parallel

data are divided into the three Chl *a* levels—low (0 to <2 μg Chl *a* L^{-1}), medium (≥2 μg to <5 μg Chl *a* L^{-1}), and high (≥5 μg Chl *a* L^{-1})—it becomes apparent that Chl *a* concentration affects the scaling relationships and the scatter observed (not presented). The variability of broadcaster and sac-spawner weight-specific fecundity and growth decreases moving from low- to high–Chl *a* concentrations. This is also observable in the general Michaelis–Menten relationships, where much scatter is observed at low–Chl *a* levels prior to saturation (Fig. 3) but less at higher Chl *a* levels. This phenomenon can be observed in many individual studies of species and is not unique to that presented here. This pattern might be expected given the high slope in the relationship over the low–Chl *a* range. Factors such as prey switching and the use of non–chlorophyll bearing prey when phytoplankton levels are lower may also act to exacerbate apparent variability in rates at low–Chl *a* levels. Our results lead us to predict that while scaling of both weight-specific fecundity and growth will be strong and significant in Chl *a*–rich areas and seasons (except in juvenile sac spawners), we predict it will be weak or insignificant in more Chl *a* dilute environments and seasons.

Although we find a positive scaling for adult sac spawners in situ, it is negative under laboratory food saturated conditions (Fig. 7); ANCOVA analysis reveals that the slopes are not parallel (Table 7). We recognize that there are few in situ data points with body weights >10 μg C ind^{-1}, and for food saturated conditions data are very limited at <2.3 μg C ind^{-1}. Weight-specific fecundity rates of the small genera *Oithona* are relatively low, and both the small sac spawners Oithonidae and Oncaeidae do not produce feeding currents and have much lower daily rations than similar sized suspension feeding calanoids (Price 1988). Oithonidae are more reliant upon motile prey and are also less mobile themselves than many calanoids. Rates for medium body weight sac spawners such as *Pseudocalanus, Clausocalanus,* and *Eurytemora,* all of which are calanoids, can be much greater than for *Oithona.* However, the very large often carnivorous sac spawners such as *Euchaeta* have very low weight-specific fecundity rates. We include laboratory food saturated rates for the carnivorous *Euchaeta norvegica* (body weight 722 μg C) at 0.023 d^{-1}. There are other larger sac-spawning species, e.g., *Paraeuchaeta, Euchirella, Pseudochirella, Gaidius, Euaugaptilus,* and *Valdiviella* (*see* Ohman and Townsend 1998); these are either strong migrators and found only rarely in the epipelagic zone (the area to which this study is limited) or are more typically mesopelagic or bathypelagic. None of these are included in either the food saturated or in situ data, although we have no reason to believe that these large-bodied sac spawners do not have low weight-specific fecundity rates too. Scaling in adult sac spawners might therefore be expected to be dome shaped, with highest weight-specific fecundity rates at medium body sizes. Because of the difficulties associated with insufficient data, care must be taken at this stage in comparing scaling between food saturated and in situ data for the sac-spawning adults, and we therefore do not assess the degree of food limitation in this group.

Increasing food limitation with increasing size has often been suggested to be the cause of negative scaling in weight-specific fecundity and growth (Hopcroft et al. 1998). Usually there are insufficient data in any one study to resolve whether the decline is a result of increasing food limitation with size or is simply intrinsic. However, we can address this issue by comparing the food saturated rates with the in situ data (Fig. 7). First, negative scaling occurs even under food saturation in the broadcasters. Although the slopes of food saturated and in situ data appear to diverge for adult broadcast and sac spawners and for juvenile broadcasters, ANCOVA analysis reveals that the slopes of in situ and laboratory food saturated rates in each of these groups are statistically parallel (Table 7). Hence, at this stage we do not find evidence for food limitation increasing with body size of animals.

Adult broadcasters under laboratory food saturation have very similar rates of weight-specific fecundity to food saturated juvenile growth of a similar body size (compare Fig. 7B and 7C); however, in nature adults seldom approach their saturated rates. What is striking is that food limitation is so much greater for adult weight-specific fecundity than for juvenile growth. Juveniles of a single species are invariably smaller than their adults, while food limitation markedly increases between these stages, but this is much more than might be explained simply by size differences alone. Indeed between-species comparisons of juvenile and adult broadcasters with similar body sizes grow at very different rates in situ, with the juveniles much closer to their maximum (*see Figs. 6 and 7*). Thus, while a broadcast adult of 10 μg C ind^{-1} has a weight-specific fecundity rate that is 35% of the food saturated value, a juvenile broadcaster of this weight has an in situ growth rates that is 72% of the food saturated rates. We return to this topic later.

In the study of Richardson and Verheye (1999) on the southern Benguela upwelling system, maximum growth rates scaled against body weight have a lower slope than mean growth rates. However, their data are a mix of juvenile (their smaller body weight animals) and adult broadcasters (their larger body weight animals). Mean rates of adults are a much lower proportion of the maximum rates, while for juveniles mean rates are much closer to the maximum rates. Thus some of the shift from a steep slope under average conditions (more food limited for adults than juveniles) to a shallower slope under maximum rates (presumably closer to food saturation for both) that they observe is likely a consequence of mixing adults and juveniles in a single relationship, with each being food limited to a different degree. This raises an important point—scaling is influenced not only by trophic conditions but by the relative mix of stages and spawning types.

Relationships to chlorophyll a *concentration*—It is not surprising that the Michaelis–Menten relationships for broadcasters using Chl *a* as the food term are significant ($p < 0.0001$). Many broadcasters are strongly herbivorous (*see* Mauchline 1998) or at least highly dependent upon food sources containing Chl *a.* Adult sac spawners demonstrate an insignificant Michaelis–Menten relationship (data first corrected to 15°C and a body weight of 10 μg C ind^{-1}), although the backward step-wise regression, for which there is no temperature or body weight correction, reveals a sig-

nificant positive relationship between $\log_{10}$ weight-specific fecundity and $\log_{10}$ Chl *a*. In comparison to the broadcasters, some sac-spawning species such as *Oithona* spp. may be more reliant upon non–Chl *a* bearing particles or size classes of Chl *a* bearing particles that do not relate well to the total term we use. For this group, Chl *a* may therefore not always be a good measure of the food available and its quality. In the future as more data become available for other food proxies these may be shown to be improved predictors/descriptors.

While broadcaster adults have a half-saturation of weight-specific fecundity constant (K_m) of 5.94 μg Chl *a* L^{-1}, for growth in their juveniles this is an order of magnitude lower, at 0.59 μg Chl *a* L^{-1}, and for juvenile sac spawners it is just 0.02 μg Chl *a* L^{-1}. Frost (1985) found egg production by the broadcaster *Calanus pacificus* to saturate at much higher food concentrations than the sac spawner *Pseudocalanus* sp. Herein we find the genera *Calanus* has the highest half-saturation constant of any of those examined, at 10.71 μg Chl *a* L^{-1}, while *Pseudocalanus* has the lowest at just 0.8 μg Chl *a* L^{-1} (Table 5). Indeed, the K_m values for the different genera are found to rank according to body weight: the larger the body weight the larger the K_m. Lower food concentrations (as measured for example as lower Chl *a* levels) affect early stages of copepods less than the later and larger copepod stages both in the field (*see* Hutchings et al. 1995; Peterson and Hutchings 1995; Richardson and Verheye 1999) and laboratory (Vidal 1980). For example, Richardson and Verheye (1999) found that 90% of the maximum weight-specific fecundity rate of the small species *Centropages brachiatus* (body weight 25 μg C ind^{-1}) was achieved at just 4.8 μg Chl *a* L^{-1}, while for the much larger *Calanoides agulhensis* (body weight 202 μg C ind^{-1}) this was only achieved at 15.4 μg Chl *a* L^{-1}. They also demonstrated that large broadcasting species grew more slowly than smaller ones, while proportional increases in growth rates between Chl *a* levels ≤ 2 μg Chl *a* L^{-1} and levels >2 μg Chl *a* L^{-1} were positively related to body size. *Calanus agulhensis* N6 increased growth by just 20% when comparing average rates between low- and high–Chl *a* categories, while adult *C. agulhensis* increased by 220%. Again, broad expectations from our grouping of a global data set are not in contradiction to the observations in a specific environment.

By contrast to our preliminary findings of K_m increasing with body weight for the few taxa for which we had data on, Hansen et al. (1997) found no evidence of scaling in K_m values for ingestion across body size for a wide range of planktonic organisms (including flagellates, dinoflagellates, ciliates, rotifers, meroplanktonic larvae, cladocerans, and copepods). In both our study and that of Hansen et al. (1997), only a few copepod species/genera are examined. We attempted to examine scaling of K_m with body weight by dividing the data set in order of magnitude body weights and deriving Michaelis–Menten relationships in each of these; this was completed separately for adults and juveniles and sac and broadcast spawners. However, the results are inconclusive, with no clear changes in any group with body weight. More work is needed before more definitive conclusions as to scaling of these measurements can be made.

Many individual studies have demonstrated growth by juveniles to be much closer to food saturation than weight-specific fecundity is to saturation in their adults (Peterson et al. 1991; Richardson and Verheye 1999). We are able to demonstrate this on a much greater set of observations in a wide range of environments. Moreover, we demonstrate the situation to be more complex, since it is confounded by temperature. Although when they are food saturated adults can achieve similar weight-specific fecundity rates to the rates of growth achieved in juveniles of similar body sizes at similar temperatures (*see Figs. 6 and 7*), Chl *a* levels must be much higher to saturate the adults than the juvenile (e.g., compare K_m values in Table 5). Furthermore, it would appear that these high levels become increasingly unlikely to be met on average for adults in natural waters with higher temperatures, while they continue to be met for juveniles. An issue of contention has been whether it can be assumed that juvenile growth is equal to adult weight-specific fecundity (Berggreen et al. 1988). Such an assumption in part underlies why we continue to perform adult fecundity measurements as indicators of copepod production in marine environments. The results here show that while the two are indeed broadly equal under food saturation, in situ rates of adult weight-specific fecundity do not on average equate to juvenile weight-specific growth, making such an assumption of equity is increasingly erroneous at higher temperatures and at Chl *a* levels below adult saturation. We suggest, therefore, that workers do not rely upon the egg production method to quantify secondary production rates of copepods; when juveniles make up an important contribution to the biomass of copepods, which is often the case, we may be dramatically underestimating secondary production if we simply rely upon growth rates derived from adult fecundity.

The Michaelis–Menten relationships are not significant for the adult sac-spawner group (Table 5), and there is not a strong decline in their weight-specific fecundity rates moving from high- to low–Chl *a* environments as there is for the broadcasters (compare the two groups in Fig. 3). A tail of low weight-specific fecundity values at low–Chl *a* levels is very obvious in the broadcasters but is absent for the sac spawners. Indeed, in the latter, rates of weight-specific fecundity below 0.004 d^{-1} are remarkably rare. Zero values are found for sac spawners, just apparently not intermediate values between 0 and $\sim$0.004 d^{-1}. While broadcasters may produce small numbers of eggs over time, sac spawners generally have a lower limit to the number of eggs that they will produce in a clutch (and thus minimum weight also); this together with the fact that they continue to produce eggs in low–Chl *a* environments may act to ensure that low growth values are uncommon.

When animals are both growing and producing eggs close to food saturation, we might expect these rates to be strongly temperature dependent. When they are strongly food limited, temperature relationships may be expected to be much weaker. Juveniles in nature are growing much closer to food saturation than their adults. The Michaelis–Menten relationships partially explain this observation. Food saturation is reached at much lower Chl *a* concentrations for juvenile weight-specific growth than adult weight-specific fecundity. This may be simply because juveniles have the ability to saturate growth at lower food concentrations than adults;

however, it may also be more complex than this. On a global scale the percentage contribution of smaller (picoplankton) phytoplankton decreases as total phytoplankton biomass increases (Agawin et al. 2000), and in regional systems large phytoplankton cells dominate as total Chl *a* levels increase (Richardson and Verheye 1998). Hence, the saturation at relatively low–Chl *a* levels in juveniles may be a consequence of their availability to prey upon smaller items than adults. The Chl *a* levels needed to attain half-saturation of weight-specific fecundity and growth suggest that food limitation may be more common for adults than for juveniles and generally more so for adult broadcasters over some sac spawners. As a consequence of the poor saturation abilities of adult broadcasters, it might be expected that in nature they would have much more variable rates of weight-specific fecundity than juvenile broadcast and sac spawners would have with regard their growth, and this is exactly what we observe (Fig. 4). Indeed, in temperate systems greater variability has been observed in the fecundity of broadcasters than sac spawners both temporally (e.g., Frost 1985; Kiørboe and Nielsen 1994; Sabatini and Kiørboe 1994) and spatially (e.g., Nielsen and Sabatini 1996). Small sac-spawning cyclopoids have been found to maintain constantly high rates of fecundity and growth in low–Chl *a* conditions (Sabatini and Kiørboe 1994). The abundance and biomass of sac spawners may be more spatiotemporally equitable than broadcasters (Paffenhöfer 1993), presumably as a result of both the more ready saturation of growth (and fecundity), but also because of their less variable egg mortality rates (Hirst and Kiørboe 2002). Although most broadcasters achieve half-saturation of weight-specific fecundity at much higher Chl *a* levels than the sac spawner *Oithona,* their maximum rates can be higher too (Fig. 4). Where Chl *a* is very low for long periods (e.g., polar oceans) and when it is continually low (e.g., oligotrophic nutrient poor open ocean), we might expect the importance of sac spawners such as *Oithona* to be increased. In fact dominance by many sac spawners in low-chlorophyll open ocean environments has previously been commented upon (Calbet and Agustí 1999). *Oithona* appears to grow well in very low- and high–Chl *a* environments; by contrast many broadcasters clearly do better when levels are higher. Where Chl *a* levels are high, either continually or for long periods, broadcasters may be able to grow faster than many of the sac spawners (compare the general and genera-specific Michaelis–Menten relationships between the two groups) and may therefore be expected to dominate the biomass. High productivity spring and upwelling blooms are often dominated by very large herbivorous broadcasters such as *Calanus* or *Calanoides* (e.g., in upwelling areas, Peterson 1998; in polar waters, Woodd-Walker et al. 2002). In more polar environments with a short season, these larger animals are often forced to rely upon body-lipid reserves and diapause outside the most productive periods. Expectations based upon the results would be that these genera would do relatively poorly in year-round low–Chl *a* environments in comparison to many other genera.

Food limitation and factors of control—Egg hatch rates of sac spawners have a similar Q_{10} to food saturated weight-specific fecundity, while both are much greater than for in situ rates. It is, therefore, not the egg hatch time itself that must limit in situ weight-specific fecundity in sac spawners, but food. Furthermore, the fact that sac spawners carry their eggs until hatching does not appear to affect the magnitude of adult weight-specific fecundity, since sac spawners achieve comparable rates to the broadcasters. Sac-spawner fecundity as eggs per female per day is much lower than in broadcasters (Hirst and Kiørboe 2002), but since the eggs are larger this explains these differences. The size of the egg sacs that the animal can carry and the mechanism that controls the size of the eggs a species produces may be most important. As a result of increasing food limitation with increasing temperature, the number of eggs per clutch will decrease and/or the interspawn period will increase in comparison to those at food saturation. Indeed, in situ egg production rates are also increasingly food limited with increasing temperature (pers. obs.).

There has been an ongoing debate as to whether fecundity and growth rates are more dependent upon food or temperature (Huntley and Lopez 1992; Kiørboe 1998). With our data set we can address these issues at the large scale of this study. Temperature explains more of the variance in juvenile growth than in adult weight-specific fecundity, and more in sac than broadcast spawners, whereas temperature explains 50.6% of the variance in juvenile sac spawners, this is 13.9% in juvenile broadcasters, but only 3.3% and 5.7% in adult broadcast and sac spawners, respectively (Table 3, Fig. 3). This is a consequence of juvenile growth rates being closer to food saturation in nature than adult weight-specific fecundity rates, while sac spawners are closer to saturation than broadcasters. On the global scale adults are much more food limited than juveniles, and their weight-specific fecundity is more dependent upon food than upon temperature, except possibly at low temperatures. Spatiotemporal variability in the weight-specific fecundity of adults should be increasingly driven by food as temperature increases. Of course the range and magnitude of temperature and food will also dictate which apparently drives variation in growth. Spatiotemporal variability in juvenile growth should be less than in adult weight-specific fecundity, although some of this may simply be a consequence of their absence during periods when their growth might be low. Furthermore, we might expect correlations between growth/fecundity and food across an area or over a season to be much weaker in juveniles than for adults. Indeed, this has been observed in regional studies (Shreeve et al. 2002).

A key finding of this work is the observation that the degree of food limitation in nature increases on average with increasing temperature for adult weight-specific fecundity. In situ weight-specific fecundity rates are on average 22% and 24% of food saturated rates at 20°C in broadcast and sac spawners, whereas they are >65% of food saturated rates at ~0°C. ANCOVA tests confirm that in situ and food saturated slopes are not parallel in adults (Table 7). This temperature effect on the degree of food limitation is not marked in juveniles, and their growth is close to food saturation through the temperature range (indeed, in broadcasting juveniles the slopes of food saturated and in situ growth versus temperature are parallel, Table 7). Smaller phytoplankton contribute more in warmer nutrient poorer waters (Agawin et al. 2000),

and, although small phytoplankton can be important in cold waters, blooms of large phytoplankton in such waters are often exploited in the life cycles of copepods during their epipelagic phase to fuel growth and reproduction events (our data are confined to the epipelagic zone). Juveniles are smaller than adults, and smaller copepods prey upon smaller particles (Hansen et al. 1994). It could be this ability that allows juveniles in nature to escape some food limitation that adults cannot. However, we are uncomfortable with this single simple explanation. A remarkable observation in the data is the marked difference between adult broadcaster food saturated and in situ weight-specific fecundity rates, while in juveniles weight-specific growth is similar under both food saturated and in situ conditions. This is not simply a result of large animals being more food limited than small animals (as one might expect from our previous argument), since juveniles of a similar size to adults grow much closer to their food saturated rates than adults do with regard their weight-specific fecundity (Fig. 7). The greater difference between in situ and food saturated weight-specific fecundity in adults is likely not a consequence, therefore, simply of their size and the consequences this has on food available. There are two further reasons for these patterns that we must present. First, later stage animals tend to grow slower than younger stage animals (Kiørboe and Sabatini 1995), and adult weight-specific fecundity saturates at much higher food and Chl *a* levels than juvenile growth. Could it be that the specific requirements to produce eggs are much more dilute in the food they consume? If juveniles and adults of similar body weight take similar types and quantities of prey (and we are not aware of enough data to test this), then the difference must relate to the quality of the food and specifically its ability to fuel the different forms of adult weight-specific fecundity and juvenile growth. Some compounds have been shown to correlate well with rates of fecundity and, hence, may be indicative of their supply controlling natural rates of egg production in copepods. These compounds include amino acids (Kleppel et al. 1998) and fatty acids (Pond et al. 1996), especially polyunsaturated fatty acids 20 : 5(n-3) and 22 : 6(n-3) (Jónasdóttir et al. 1995). The ratio of seston 20 : 5(n-3) to carbon relates closely to daphnid growth rates in fresh waters (Müller-Navarra et al. 2000). These issues need to be more fully explored in marine waters, since they could hold the key to understanding not only adult fecundity and productivity but also potential recruitment.

There is another explanation as to the differences in weight-specific fecundity and growth achieved by adults and juveniles. Food limitation acts differently on fecundity, juvenile growth, and development rates in nature. At the individual level, food commonly limits adult female weight-specific fecundity (and fecundity) such that recruitment as eggs is below the food unlimited maximum rate. Stage duration and molting rate are physiological processes that are primarily dictated by temperature and altered less by food. At the level of an individual juvenile, not only does food limitation act to reduce growth, but under severe limitation it may also control whether individuals survive or not. Juveniles that do not gain a sufficient quantity of weight between molts (i.e., within a relatively strictly predetermined period) do not survive (Lopez 1991; *see* concepts in Carlotti and Sciandra 1989). By contrast, adults need sufficient ration to meet metabolic demands or they can live off food reserves, but they do not need to produce eggs to survive. This may explain why juvenile growth rates rarely fall below 0.01 d^{-1}: juveniles rapidly become extinct when growth rates are too low. By contrast, rates of weight-specific fecundity for adults very commonly fall well below this level, and adults do not die as easily as a result of low food. Food limitation may effectively act as a filter for juveniles; those individuals not gaining sufficient weight before the next molt, and hence growing at lower rates, are removed from the population. Of course as an extreme this would mean all individuals would eventually be removed; we might rarely find such individuals because of their short residency, and they would be likely in the rarely studied early nauplii feeding stages. Importantly, this explanation does not negate the fact that a population of juveniles does saturate their growth at lower food concentrations; these observations are still true, simply lower food also involves the removal of those individuals from the population that are not able to achieve sufficiently high growth rates. The rules that govern how much weight is need to be put on within a stage need clearly be known in different species and in relation to body weight and temperature. The two alternate views we have presented here are not mutually exclusive, but both need urgent attention since these will underpin what controls the numbers, biomass, and distribution of a key group of planktonic organisms.

The development times we present may be biased as a consequence of how we measure development (Carlotti and Nival 1991; Hirst and Sheader 1997); furthermore, only individuals that make it from egg to adulthood can by definition be included in the measurement. Thus, for example, under severe food limitation or when mortality rates are too high and animals do not reach adulthood, development time cannot be measured. Since such development times are even more affected by mortality than the short-term juvenile growth rate measurements, food saturated and in situ rates are closer for development than for growth.

Rates of in situ weight-specific fecundity of adults and weight-specific growth of juveniles diverge with increasing temperature. This may suggest that mortality of juveniles as a result of not attaining sufficient weight during the intermolt period increases with increasing temperature (since presumably fewer individual juveniles are able to gain weight at a sufficient rate). Indeed, juvenile mortality does increase with temperature according to the predictions of Hirst and Kiørboe (2002). We are also led to the conclusion that in natural waters not only will initial recruitment (as egg production) decline with declining Chl *a* levels for the broadcasters (but not so strongly for many sac spawners), but mortality of juveniles caused by food limitation will also increase along such a gradient. This prediction is not at odds with the steady-state approach of Hirst and Kiørboe (2002). Although total mortality rates must decline from food-rich areas into low food areas as they suggested (much of which will arise from changes in predation mortality), the subset of total mortality that arises from this food-limitation effect may therefore have the opposite slope. These predictions now need to be tested in the natural environment.

Model equations—The empirical models derived here give us a better ability to predict weight-specific fecundity and growth rates and understand the patterns. The significance of the Michaelis–Menten plots of growth versus total Chl *a* concentration and the multiple linear regression analysis suggests that Chl *a* is a good first approximation as a food proxy relating to weight-specific fecundity and growth in broadcasters. The relationships we present could be used to predict and map copepod production from measurements of their size distributed biomass, temperature, and Chl *a*. These parameters can be easily measured at high resolution over large areas using modern oceanographic equipment. If we compare each measured value in the database with predictions using the group-specific multiple linear regressions, then predictions fall within a factor of two of the measured values (i.e., between 0.5 to 2 times the measurements) on 67% and 78% of occasions for juvenile broadcast and sac spawners and 35% and 49% for adult broadcaster and sac spawners. These are significant improvements on the prediction abilities of previous models.

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